Mesozoic Coleoptera

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This monograph is a major treatment of Mesozoic Coleoptera, being the first review of the evolution of beetles during that era. The Early Mesozoic, Late Mesozoic and Late Cretaceous stages are recognized in the phylogenesis of Mesozoic Coleoptera. Special attention has been paid to their ecological associations, particularly with food plants. One hundred and eleven species, 64 genera and 19 families are described, of which all species, most of the genera and four families are new.

This work is of interest to entomologists and paleontologists, especially paleobotanists and stratigraphists of Mesozoic continental deposits.

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Scientific Editor
Natalia J. Vandenberg

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Plates 14, illustrations 109, bibliography 58 entries.

Editor-in-chief

B.B. Rohdendorf
Doctor of Biological Sciences

Foreword to the English Edition

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

The present edition is a translation of a major collaborative work on Mesozoic fossil beetles written by four eminent Soviet scientists. This is the first time that detailed descriptions based on the exceptionally fine collection of the Paleontological Institute, Academy of Sciences, USSR, have been made accessible to English-language readers. The Institute collection contains over 15,000 specimens of fossil beetles from the Triassic, Jurassic and Cretaceous, including many key examples exhibiting a remarkable state of preservation.

The Mesozoic Era marks a crucial period in the evolution of beetles: at its commencement we encounter some of the first examples of specimens possessing characteristics suggestive of particular suborders of Recent Coleoptera, and by its close, many modern families may be found among its diversified fauna. The scope and importance of the present work is discussed by B.B. Rohdendorf in the brief abstract and foreword to the Russian edition, and will not be repeated here. However a few comments relevant to the English-language edition are in order.

The translated version of *Mesozoic Coleoptera* has remained as faithful as possible to the original work, but what we have attempted here is a translation of ideas, not of words. In many instances a departure from a more *verbatim* style was necessary in order to preserve meaning. This was particularly true of the narrative portions of this work where we took the liberty of breaking up some of the longer sentences and, occasionally, of rearranging the sequence of ideas. Sometimes additional information which had been implied but not strictly stated in the Russian text was added to the translated version either in brackets or as a footnote. Russian terms which represent a translation of Greek or Latin taxonomic categories were treated as equivalent to the latter. For example, the term "zhestokokrylye" was translated as the scientific ordinal name "Coleoptera," not as "sheath-wings" (a literal translation) or "beetle" (the common name). Proportional measurements are reported in a format which we hope will make them more comprehensible to English speakers; their treatment is discussed in a brief footnote at the beginning of the *Descriptions of taxa* section.

The English-language edition of *Mesozoic Coleoptera* was initiated at the request of Terry L. Erwin, Curator of Coleoptera at the National Museum of Natural History, Washington, D.C., and published by the Smithsonian Institution Libraries in cooperation with the National Science Foundation. Many people have contributed towards the preparation of this publication. In addition to the key individuals whose names appear within the covers of this book, I would like to thank the many people who have helped with the translation, coordination and production of this edition. I would also like to thank my father, George N. Vandenberg, for his assistance in interpreting some of the Russian idioms, and my colleague Alan I. Kaplan for the loan of pertinent literature from his private library.

July 1989

Natalia J. Vandenberg, Ph.D.
Scientific Editor
Albany, California

Foreword

3 Coleoptera are distinguished from other organisms by their exceptional diversity. The number of present-day species in this order not only exceeds that of any other order, but of all plants and animals combined, excluding insects. Beetles play a significant ecological role and are economically important as crop and stored-products pests. Our present knowledge of the structure, ecology and taxonomy of Coleoptera is fairly advanced, but information on their evolution (i.e. actual stages in the formation of the group) is highly inadequate. Study of the geological history of beetles is important not only for a description of their phylogeny and classification, but also, in a broader sense, for understanding many trends in the evolutionary process.

From the end of the Paleozoic era, Coleoptera have played a vital role in continental biocenoses. Moreover, in the Early Mesozoic their role was probably even more important than at present. Data on ancient beetles are also important for an understanding of trends in the formation and functioning of ancient biocenotic complexes. At present, our knowledge of ancient beetles is totally inadequate. Almost all information pertains to Cenozoic beetles which are poorly distinguished taxonomically from present-day forms, belonging to the same families and, in many instances, even to the same genera. The entire protracted period of their early history—the end of the Paleozoic and particularly the whole Mesozoic—remains inadequately studied to date. This has generated increased interest in ancient Coleoptera, particularly Mesozoic ones.

Entomological studies conducted since the 1920's on a variety of Mesozoic faunal complexes in the USSR have provided abundant coleopteran material. This material has been greatly enriched in the last decades and, more importantly, its quality has vastly improved since attention focussed on the search for intact whole fossils during field studies. Most early descriptions of Mesozoic Coleoptera were based on the study of a
4 single elytron or other fragments; these were not sufficient to permit an exact determination of the insects' taxonomic affinities. Present-day studies of complete fossils of ancient Coleoptera have made it possible to reliably recognize their characteristics. Following the study of individual groups of beetles, conducted by specialists of each order, a detailed account of

Mesozoic beetles could be compiled together with outlines of the faunal complexes of Mesozoic Coleoptera.

The review of Mesozoic Adephaga is particularly important and includes descriptions of 56 species, 31 genera and 8 families. Literally for the first time, phylogenetic trends within the suborder are evaluated using primarily new material, and taking into account diverse ecological and functional characteristics (A.G. Ponomarenko). This matter is considered relatively fully in the description of Adephaga. The large suborder Polyphaga, on the other hand, is treated more unevenly. For example, the unexpectedly large chapter on the Rhynchophora (33 species, 18 genera, 3 families), specialized beetles which are usually placed at the end of the system even though they are rather well represented in the Mesozoic material (L.V. Arnol'di and V.V. Zherikhin). Important are the descriptions of some Early Cretaceous Scarabaeidae (L.M. Nikritin) which until recently were practically unknown from the Mesozoic. Finally, some phylogenetically interesting Polyphaga are described, for example, the aquatic Hydrophiloidea (8 species, 5 genera, 2 families); the taxonomic positions of many of these are uncertain (A.G. Ponomarenko). Equally interesting are taxonomically isolated Cucujiformia (3 families) that permit some generalization (V.V. Zherikhin). On the whole, this volume is a major new treatment of a widely distributed and important group of Mesozoic insects. It allows the development of various conclusions and comparisons regarding ecology and evolution of the continental fauna of the earth.

B.B. Rohdendorf

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Introduction

5 Of all stages of the historical development of beetles the Mesozoic is the most difficult to study. Paleozoic beetles, whose remains are found only in the Permian deposits, were apparently rather less numerous and diverse. So far only 200 or so coleopterous remains have been collected from the Permian continental strata. The remains of the Permian beetles are much more abundant in regions thought to have had a temperate climate. No Permian beetles have been found, which could be assigned with certainty to the more advanced suborders. All of them either definitely are members of the suborder Archostemata or can belong there. To date, 32 genera of Permian Coleoptera belonging to 5 families have been described. It is true that most of them have been established from a single elytron, however the evolutionary characteristics of Permian beetles enable us to consider the taxa established from single elytra as fairly natural (for further details see Ponomarenko, 1969). The limited diversity of Permian beetles and the fact that their evolution can be followed even from isolated sclerites, simplifies the task of describing them and of studying their historical development.

The study of Cenozoic beetles has been similarly facilitated although for another reason. Cenozoic Coleoptera differ very little from extant forms, belonging to the same families and, in many instances, even to the same genera. This makes it possible to differentiate them using indirect diagnostic features which are often more highly visible on fossil remains than are the key characters that accurately establish their taxonomic position.

The study of Mesozoic beetles is a more complex problem. On the one hand, the Mesozoic beetles are almost as diverse and numerous as the extant beetles. At any point of time in the Late Mesozoic, these beetles were certainly represented by hundreds of thousands of species belonging to over a hundred families (there are almost 200 families of extant beetles). Thus in a single Jurassic site of Karatau, the family Cupedidae is represented by 20 species (Ponomarenko, 1968b), Eobelidae by 30 species (Arnol'di, this monograph), and Elateridae by more than 20 genera (Dolin, 1975) with perhaps about 100 species.

On the other hand, most Mesozoic beetles belong to extant families or those closely related to them. However, representatives of the contemporary families usually differ so markedly from Cenozoic* ones that the use of indirect diagnostic features becomes unreliable. Intact and well-preserved remains are therefore a prerequisite for determining the taxonomic position of Mesozoic beetles since important taxonomic characters can be studied in them (e.g., the structure of antennae, propleura, base of the abdomen, hind coxae, and the number and arrangement of abdominal spiracles).

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*From the context it seems likely the word "Mesozoic" was intended—Scientific Editor.

Unfortunately, practically none of the earlier described remains of Mesozoic Coleoptera meet these requirements. For most of them, the taxonomic position indicated by the author was not substantiated at all or was
6 substantiated only by indirect characters and external similarities. The remains of an excellently preserved beetle, *Proteroscarabeus yeni* Grabau, were studied by two researchers (Grabau, 1923; Ping, 1928). All the same, the description contains no characters that formally justify its inclusion in the family Scarabaeidae. Hence the Mesozoic history of beetles remains almost totally unexplored even though nearly five hundred beetles have been described from this era.

The foregoing explains the interest in almost any publication dealing with fairly complete remains of Mesozoic beetles. Particularly important is the study of the vast collection of Mesozoic beetles preserved in the Paleontological Institute, Academy of Sciences, USSR. This collection includes over 15,000 remains of Triassic, Jurassic and Cretaceous beetles and evidently exceeds all other collections of Mesozoic beetles combined. This collection includes many examples of exquisitely preserved ancient beetles in which not only integumental structures, but also other characters rarely available to the paleontologist can be studied (e.g., the structure of the hind wings, mouth parts and endoskeleton). These latter characters permit speculation about specific musculature.

Unfortunately, this magnificent collection remains poorly studied. Earlier, only archostemate beetles have been investigated in great detail (Ponomarenko, 1964, 1966, 1968a, b, 1969) and three other papers have been devoted to major groups of beetles from the Jurassic site of Karatau (Tikhomirova, 1968; Medvedev, 1968; Dolin, 1975). The remaining papers contain descriptions of only individual forms of Mesozoic beetles.

The present work, as well, does not present an exhaustive description of Mesozoic Coleoptera, even of those solely from the collections of the Paleontological Institute. Only Adephaga were examined in considerable detail. From this suborder, 58 species covering 32 genera and 8 families are described below. Three families, 28 genera and all the species are new. Aside from the Mesozoic beetles described here, less than 10 genera are known which can be definitely included in the Adephaga. Most of the taxa in the present book are described from adult beetles and only two species from larvae. However, the volume of material on these two larvae is almost as large as that on the adult beetles: in all, nearly 150 adults and 100 larvae. Based on the Mesozoic adephagan material studied, it was possible to describe in general terms the characteristics of the Mesozoic stage in the evolution of these beetles.

In this work, beetles of the suborder Polyphaga are presented in individual groups. Only a small proportion of the representatives from this gigantic group, present at the Paleontological Institute, have been described. However, some tentative ideas can be developed about the Mesozoic evolution of Polyphaga using the newly described material combined with earlier descriptions. Only two series of superfamilies recognized by Crowson (1971) are not represented in the Mesozoic: Eucinetiformia and Bostrychiformia. The former is undoubtedly present in the Jurassic of Karatau and is represented by forms very closely related to the extant ones. The latter obviously existed in the Mesozoic; its remains must be available in collections, but, have not yet been recognized. In all, 53 species of Polyphaga belonging to 32 genera and 11 families are described below.

Some of the beetles are described from inclusions in Mesozoic fossil resins, often called ambers by analogy with Baltic amber. Beetles embedded in Mesozoic resins have been reported earlier (Carpenter, et al., 1937; McAlpine and Martin, 1969) but remain undescribed. A study of the remains of ancient beetles in the transparent resins permits their description with the same degree of detail as for the extant forms. It is a very important observation that within the resins, as a rule, one encounters minute beetles which are difficult to study from their impressions. Resins, thus considerably expand the range of information available to us on ancient insects.

Different groups of Mesozoic beetles are described here by four authors who have attempted, insofar as possible, to achieve a uniform style of presentation. However, existing traditions in the style of descriptions, and
7 even in the morphological nomenclature of different groups, preclude complete uniformity. All the described material is preserved in the Paleontological Institute, Academy of Sciences, USSR (PIN). Some important principles in the study of fossil beetles have been stated earlier (Ponomarenko, 1969b) and do not warrant rediscussion. The exact taxonomic positions are far from being established for many of the described forms. Such forms have been placed in a separate genus only when substantial evidence indicated that they could not belong to any extant or extinct genus. When such a demonstration was not possible, the remains were described as a formal collective genus named after the type genus of the family with the suffix "ites". In some instances, formal genera were proposed for fragmentary fossils. Since a formal comparison of these forms is not possible, the section "Comparison" in their description has been replaced by "Taxonomic position" to discuss the probable taxonomic status of the fragmentary form. The material studied originates from sites repeatedly described and discussed in the literature. Hence they have not been described here; their description can be found in earlier papers (Ponomarenko, 1969; Rasnitsyn, 1969, 1975).

The main faunal complexes of Mesozoic coleopterans are characterized in a very brief and concise form. Unfortunately, their analysis was possible only for the territory of the USSR. The rather numerous fossil beetles known from other territories are almost totally inadequate for comparison because of imperfect descriptions. Naturally the documented Mesozoic history of beetles is fragmentary and does not give a complete picture of the Mesozoic evolution of beetles; it presents only individual moments of this history.

Composition and Ecological Characteristics of Mesozoic Coleoptera

8 As previously mentioned, the sites of Mesozoic beetles are very unevenly distributed over the earth. Rich sites, yielding an abundance of suitable study material, are even more unevenly distributed. A large proportion of the fossils of ancient Coleoptera consist of isolated elytra; but, unfortunately, in the Mesozoic these only rarely provide a basis for ascertaining the taxonomic position of the beetle. In the future, when our knowledge of ancient beetles has increased considerably, it will be possible to determine the taxonomic position of incomplete fossils and use them for paleobiogeographic and biostratigraphic purposes. For the present, well-preserved fossils are absolutely necessary. Only 1–10% of the fossils collected from various sites are useful for study, but hundreds and thousands of specimens from a given site are necessary for any valid judgement on beetle complexes.

The potential that any site offers for analysis depends greatly on its taphonomy. In some sites, more or less intact beetles are preferentially buried and sometimes the number of entire impressions may even exceed the number of isolated elytra. In other sites the remains get dislodged and dismembered before burial so that the number of entire specimens is reduced to only a small percentage. The first type of site is highly promising for investigation, but when dealing with the second type of site, thousands of remains need to be collected in order to obtain the required material. Even collections of many isolated elytra are not entirely useless. Each separate elytron may not be identifiable but the overall spectrum of morphological types of elytra and their quantitative relations often turn out to be highly significant.

Few of the Mesozoic sites have a potential value of the study of ancient Coleoptera. This is despite the fact that during the Mesozoic, beetle remains are most numerous in oryctocoenoses, and the Mesozoic fossil insect sites number in the hundreds. The problem is well illustrated by a recent attempt to re-examine the type material from the well-known site of Mesozoic insects at Solenhofen in the Federal Republic of Germany (Ponomarenko, 1971a). The preservation of the fossil remains in this site has always been considered exemplary but in the studied collection, including a large proportion of type material, there were hardly any remains whose taxonomic position could be decided with absolute conviction. In most cases it had to be simply stated that due to the poor state of preservation they were not suitable for the present investigation. The taxonomic assignments made by the original authors proved totally incorrect. Only one species has been found to actually belong to the family in which it was placed in the original description.

Presently almost all the sites yielding abundant specimens of ancient 9 beetles are located in Asia, mainly in the northern part. There are very few rich sites on other continents. The abundance of material collected in the Asiatic part of the USSR is due to two reasons. First, only in the USSR have expeditions recently been conducted by a large team of paleoentomologists for the sole purpose of collecting fossil insects. The collections from the USSR surpass the remaining global collections. Second, the inequality of sites in the European and Asiatic parts of the USSR arises from differences in their geologic structure. The nature of deposits in these territories is such that Mesozoic fossil insects are very rare in the European part of the USSR, whereas the Paleozoic collections from both territories are of the same order. Western Europe is far more favorable for the Mesozoic insect fossils but practically no special expeditions have been organized solely for fossil collection.

The faunal complexes discussed here appear rather geographically restricted and do not represent the entire global biota of the Mesozoic era. At the same time, the sites examined occur in different climatic or, in any case, floristic zones. The chronologically sequential sites are frequently found in different zones and thus it is difficult to determine the cause of such differences—their position in different zones, or evolutionary shifts. These factors inevitably influenced the nature of the investigation of the fauna described below.

The oldest Mesozoic faunal complexes—the Triassic and early Jurassic ones—sharply differ from the later complexes. In composition they are closer to the Paleozoic than to the Late Mesozoic. Almost all their constituent beetles belong to the most ancient and the most primitive suborder Archostemata. Unfortunately, beetles from the Early Triassic are extremely rare. The rich Dzhailyaucho site in southern Fergana was considered Early Triassic, and paleobotanists (Sikstel', 1962, 1965) even assigned its lower strata to the Permian. Recently I.A. Dobruskina (1970, 1974) showed that all the deposits in the Madygen area, including even Dzhailyaucho, are coeval and belong to the end of the Middle–Early Upper Triassic. Archostemata have already been described from Dzhailyaucho; astonishing differences have been observed between these supposedly Early Triassic beetles and the Late Permian ones, in addition to their similarity with Coleoptera from the known Middle and Upper Triassic sites (Ponomarenko, 1969b). A similar type of resemblance was reported by A.P. Rasnitsyn (1969) for Hymenoptera. This was ascribed to the fact that the Triassic fauna of Australia, where rich collections of Late Triassic insects are known, has a more ancient continental character than that from the northern continents. The need for such suppositions no longer exists.

As mentioned earlier, almost all Triassic beetles are Archostemata. More than 15,000 insect fossils have been collected to date from Triassic deposits in the Madygen area. Beetles occupy third place after cockroaches and cicadas. Nearly 3,500 fossil beetles have been recovered. It is difficult to establish the exact proportions of beetles of different suborders. Isolated elytra constitute the vast majority of the fossil remains of beetles from this site. Using these remains, it is not possible to distinguish the schizophoroid Archostemata from primitive Adephaga, or Ademosynidae (related to Archostemata)* from many Polyphaga. A comparison of groups must therefore be made from only a few well preserved beetles. To date, a total of 63 species (here and throughout including those described in the text) of Triassic beetles of 34 genera and 7 families have been described from Madygen. Of these, only four species definitely do not belong to Archostemata. True, some beetles belonging to Adephaga were possibly described as Archostemata. The difficulties encountered in differentiating the Mesozoic members of these beetles are discussed in the section specially devoted to the Mesozoic Adephaga, hence they are not discussed here. However, in the Triassic faunal
10 complexes, both higher suborders**, even with the most liberal estimate, do not make up the 10% estimated earlier (Ponomarenko, 1968a).

Among the Triassic Archostemata, members of the family Cupedidae are the most varied. They constitute 25% to 50% of all beetles at the various sites. From the Dzhailyaucho site alone 29 species have been described, but their diversity is by no means fully revealed. There are numerous beetle fossils that clearly do not belong to these species and remain unidentified due to their poor preservation, which precludes their formal inclusion in any particular genus. The Cupedidae first appeared in the Triassic (their fossils are not known from older deposits) and are represented by all of the three subfamilies, one of which is known only from the Triassic. In no other period have the Cupedidae been so numerous and diverse; the cupedid taxa at Dzhailyaucho far outnumber the extant taxa the world over.

The Schizophoridae with 16 species and 10 genera occupy the second position. Although their species are far less than those of cupedids, they are close to cupedids in the number of genera, and surpass them in the number of extant forms. In morphological diversity, they are on a par with the present-day ground beetles excluding the paussids. The remaining three families—Tricoleidae, Ademosynidae and Catinidae—are represented by relatively few and less diverse forms.

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*The authors' treatment of Ademosynidae is inconsistent. It is alternately placed within Archostemata or contrasted with the latter—Scientific Editor.

**Presumably Adephaga and Polyphaga—Scientific Editor.

The suborder Adephaga is represented by the unique family Triaplidae, possibly the most primitive member of the suborder. The presence of one representative of Trachypacheidae, poorly differentiated from the Early Jurassic forms, is unexpected. Hydradephaga are not found in Madygen, but in the Upper Triassic sites of Garazhovka in the Ukraine an incomplete beetle fossil has been found, which may be the form directly related to the whirligig ancestors.

Representatives of the suborder Polyphaga are even less numerous. A single form of uncertain affinities is described below which may be very close to the Dascilloidea (sensu Crowson, 1971) and is characterized by many primitive features. In addition there are several interesting yet undescribed forms. One fossil beetle, based on the shape of its pronotum, almost certainly belongs to Elateroidea. Unfortunately, the preservation is so poor that it is not possible to determine its family, particularly whether it is Praelateridae or Elateridae. Finally, three fossil beetles have been found in Madygen, whose presence in the Triassic was very unexpected: these beetles are very close to the Jurassic Eobelidae described in the text. They have a typical Rhynchophora morphology with a rather long rostrum and an oxycorynoid body with a distinct longitudinal ridge on the propleuron.

The ecological spectrum of beetles found in Madygen is also interesting. Phytophages are primarily represented by the very abundant cupedids. The Triassic cupedids differ little from the Jurassic ones; the most specialized forms, as far as one can judge from the shape of the body, are most closely related to them. Among the Jurassic cupedids there are even extant genera, hence there is no doubt that the Jurassic and Triassic cupedids hardly differed in mode of life from their present-day relatives. It would follow that they lived in wood broken down by fungi, feeding on the fungi and the decaying wood. All the Polyphaga of Madygen, except the Eobelidae, also thrived on wood, but of a far more decomposed nature. The Eobelidae were probably spermophagous. The parallel flourishing of the Eobelidae with cycadophytes suggests that the larvae of these ancient weevil-like beetles lived in cycadophyte fruits.

A large number of beetles from Madygen were in some way linked to water. All possible arguments in support of an aquatic or riparian life for most schizophoroid Archostemata have already been advanced (Ponomarenko, 1969). No new evidence has been presented either to support or contradict this point of view. These forms were probably poorly specialized aquatic or
11 riparian predators and detritovores which inhabited both sides of the coastline. Forms adapted to swimming are not found among them. There are also typical terrestrial forms, differing little in external appearance from ground beetles. They differed from the primitive ground beetles of the genus *Sogdodromeus* (Trachypacheidae), found alongside them, in having distinctly tuberculate sculpturing of the integument typical of the Archostemata. It

is possible that unidentified primitive ground beetles are present among them. The feeding habits of the Triaplidae remain unknown. Their closest relatives, the Haliplidae, are strict algivores, feeding on green and charophyceous algae. The Triaplidae were probably also phytophages or detritivores as indicated by the orthognathous or even opisthognathous head, whereas in predators the head is almost always prognathous.

The largest fossil beds of Early Jurassic Coleoptera are also distributed in Soviet Central Asia.* Unfortunately isolated sclerites, mainly elytra, predominate in all the beds, and complete fossils are very rare. Although several thousand beetle fossils have been collected, not many are suitable for study.

As before, Archostemata predominate and presently constitute one-half to three-fourths of all the beetles. Archostemata dominate also among the described species: 22 species of Archostemata have been described versus only 8 of the other beetles.

The Cupedidae, as usual, are the most widely distributed group of Archostemata. However, they now constitute not more than 10% of all the beetles, and only in one site, Kyzyl-Kiya, 26%. Triadocupedinae, the most primitive subfamily of cupedids, has not been found in the Jurassic; it is true that even the most advanced, primarily Cenozoic subfamily Cupedinae, which existed in the Triassic, is also not found in the Early Jurassic. All the cupedids known from the Early Jurassic belong to Ommatinae; the Mesozoic tribe Notocupedini accounts for 75% of all the forms found. Only 7 species of the genus *Notocupes* have been described from the Early Jurassic, but elytral diversity suggests a much higher number. The extant cupedids, *Omma* and *Tetraphalerus*, appeared in the Early Jurassic.

The remaining Archostemata are almost exclusively represented by aquatic forms. Outwardly they strongly resemble water scavenger beetles (Ademosynidae) and the rather diverse Schizophoridae. The latter retain almost all the lineages present in the Triassic but their diversity is generally markedly reduced. The number of terrestrial forms is particularly small. This is probably explained by the displacement of such forms by the very similar primitive ground beetles. Among aquatic schizophorids the appearance of very characteristic Mesozoic forms with long, hooked legs and hypognathous head is worthy of note. These beetles probably lived on the aquatic vegetation. One genus of the family Tricoleidae has also been reported.

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*The Russian literature frequently refers to two distinct geographical localities "Tsentral'naya Aziya" (Central Asia) and "Srednaya Aziya" (loosely translated as Middle Asia). The former term refers to Sinkiang Province in China (or the former Chinese Turkestan), while the latter refers to the former Russian Turkestan (the Kirgiz, Uzbek, Turkmen and Tadzhik SSR). Since there is no geographic locality by name Middle Asia, we prefer to call it Soviet Central Asia—General Editor.

At the beginning of the Jurassic, beetles of the suborder Adephaga were apparently represented by all the major Mesozoic groups, although all of them are still not known. Whirligigs and primitive dytiscoids obviously must have existed among the aquatic Adephaga, but in fact only one form, *Necronectulus*, distinctly close to the dytiscoid root, is known. A primitive fossil beetle of the family Coptoclavidae has been found in Soviet Central Asia in the supposedly Early Jurassic deposits, but recently doubts have been expressed about the correct age of these deposits: possibly they are younger. In these deposits, terrestrial Adephaga are represented by fossils of Carabidae and Trachypacheidae. These fossils represent the most primitive forms of both families.

Well preserved fossil Polyphaga are rare in the Lower Jurassic sites. At present only representatives of the Elateridae are known; or, more precisely, its Mesozoic subfamily Photagrypninae and the family Praelateridae which is closely related to click beetles (Dolin, 1973, 1975).

Unfortunately, the Middle Jurassic beetle fauna, next in chronology, has been collected almost exclusively from sites in Siberia. Hence it is difficult
12 to say if its lack of congruence with the preceding fauna is due to evolutionary changes or simply to zoogeographic peculiarities. Moreover, the beetles in these sites are represented only by aquatic or littoral* forms. Archostemata are generally not found here. This is particularly significant with respect to cupedids. Whereas other Archostemata may elude identification based on isolated elytra, this possibility is ruled out for cupedids. In all the Siberian Jurassic sites not a single cupedid elytron has yet been found. Hence their abundance must be at least two orders of magnitude lower than in the Jurassic sites of Europe and Soviet Central Asia. In Siberia, cupedid fossils were discovered in the younger Cretaceous deposits. This difference is apparently due to the characteristics of the Jurassic vegetation of Siberia, where gingkos and chekans** predominated and conifers were rare.

Adephaga turn out to be the dominant group of beetles from these sites. Even though the number of fossils collected here is not great, all the Mesozoic families of aquatic Adephaga—Parahygrobiidae, Liadytidae, Coptoclavidae and Gyrinidae—have been found in the Siberian sites whose ages are close to Middle Jurassic. Fossils of the most primitive beetle larvae—larvae of aquatic *Parahygrobia*, *Angaragabus* and *Stygeonectes*—have also been collected from these deposits.They all belong to the dytiscoid Adephaga and are hardly different from the extant dytiscoid larvae. Among them are nektonic and benthic forms. These were all air breathers, with their well developed tracheae modified to form a hydrostatic apparatus. One of the

*So given in the Russian original but by intent should read "aquatic, more particularly littoral"—General Editor.

**Apparently representatives of cycadales—General Editor.

larvae (*Angaragabus*) showed a falciform mandible, lacking a retinaculum, but with an internal canal. A larva of the staphyliniform Polyphaga, probably a primitive hydrophilid, has also been found here.

It is noteworthy that to date no representative of Geadephaga has been found at these sites. This may be considered a chance occurrence due to the poor collections, but here, as well as in two other sites, fossils have been found of a possible ecological analog of the Mesozoic ground beetles: the primitive carrion beetle *Mesagyrtes*, closest to the extant predaceous carrion beetles feeding on coastal mollusks. Fossils of this beetle constitute a third of all the collected coleopteran fossils: an absolutely unique case. Only primitive hydrophilids and staphylinids could be identified among the remaining Polyphaga. This fauna is thus almost exclusively associated with water, which makes its comparison with other fauna difficult. Interestingly, this is not an isolated discovery; similar fauna have been collected from more than ten sites spread over a vast territory from west Siberia to Trans-Baikal.

Beetles from the very end of the Jurassic are best known from the famous Karatau site in south Kazakhstan. The site is a chain of rock outcrops apparently formed in a large lake. The composition of insect fossils varies somewhat in different outcrops, but whether this is due to variations in the conditions of burial or the age of the deposits is not yet clear. More than 18,000 insect fossils have been collected from this site, also a few fossils of other arthropods and a rather large number of vertebrates, particularly fish. The collection from Karatau has more than 5000 fossil beetles. Since in recent years only the intact, well preserved fossils have been collected, in reality the number of beetle fossils could be very large*.

The composition** of beetles from Karatau differs sharply from that at the beginning of the Jurassic. The Archostemata constitute only about 10% of the beetles. Precise estimates give a high figure but this is probably an overestimate since the elytra of cupedids were collected fully, but not those of other beetles owing to poor preservation. Thirty species of Archostemata representing 13 genera and 4 families have been described from Karatau. Recent collections from this area almost doubled the number of beetles but mainly repeated previously documented finds, yielding only two or three new species. According to a preliminary estimate, the Archostemata constitute approximately 5 to 10% of all taxa; and 75% of the Archostemata are cupedids, which are particularly diverse in this site. An entire series of
13 endemic genera were restricted to the Late Jurassic or appeared only in the Early Cretaceous; these existed alongside the genera which had appeared earlier and persisted throughout the Cretaceous, a few even continuing to the present day. The remaining Archostemata—from the families Ademosynidae, Schizophoridae and Catiniidae—are unique forms and, judging from

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*Not a verbatim but meaningful translation—General Editor.

**Species composition—General Editor.

their body structure, are aquatic. Among them, representatives of the genus *Tersus* distinctly predominate. Judging from the long hooked legs, they inhabited aquatic vegetation. The large number of specimens collected may provide additional evidence of their aquatic life.

The number of accurately determined specimens of Adephaga exceeds that of Archostemata, though their actual numbers were apparently similar. Twenty-three species, 13 genera and 4 families of Adephaga have been described from Karatau. The Hydradephaga are represented by one genus of whirligigs and four genera of coptoclavids. The coptoclavid diversity is greater here than in any other site. The Geadephaga are almost twice as numerous as the Hydradephaga. The Carabidae and Trachypacheidae are almost identically represented both in the number of taxa described and the number of specimens.

Almost all Karatau beetles belong to Polyphaga. This is the most primitive fauna in which the Polyphaga are distinctly dominant and very diverse. Apparently, the entire series of superfamilies (Crowson, 1971) is represented in the Karatau collection, but it has not been possible to prove the validity of many identifications.

A few primitive hydrophilids have been found among the Staphyliniformia, including forms close to Hydraenidae. In addition, many staphylinids (nearly 200 impressions) of the most primitive subfamilies Oxytelinae* and Tachyporinae have been found; these belong to 16 species and 10 genera (Tikhomirova, 1968, 1973).

The Eucinetiformia are represented by rather abundant Eucinetidae. These differ only slightly, at least in external appearance, from the present-day *Eucinetus*.

The Scarabaeiformia are rare in Karatau. Beetles externally resembling Dascilloidea are fairly widespread but their dascilloid nature and the validity of their inclusion in the genus *Mesodascilla* (Martynov, 1925) of the Dascillidae, has not been confirmed. Representatives of Scarabaeidae are also less numerous. Only two rather poorly preserved beetles have been found. These are close to the primitive Scarabaeidae already abundant in the Early Cretaceous.

Fossils of the Elateriformia are particularly abundant in Karatau. The only strictly Mesozoic group of Polyphaga, which could be assigned the taxonomic status of a superfamily, has been found here. Its members are rather diverse in morphology and size; several dozen of them have already been found. These are closest to representatives of the recently established superfamily Artematopoidea Crowson, 1973, but are distinguished by the presence of a transverse metasternal suture. This character unites them with metallic wood borers. The latter are rare in Karatau; the number of specimens collected is less than 10. Click beetles are the most abundant group of Polyphaga, and of beetles in general, in Karatau. Nearly 250 of their specimens have been collected. They mainly belong to about 20 genera of the primitive, extinct subfamily Protagrypninae (Dolin, 1975) distributed almost exclusively in the Mesozoic. Members of the Agrypninae, Diminae, Negastriinae and Cardiophorinae are rarely encountered. Members of the Bostrychiformia have not been identified among the Karatau beetles, but are almost certainly present.

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*Given as Oxytelidae in the Russian original—General Editor.

The Cucujiformia are rather well represented in Karatau. The Cleroidea are few though diverse. The Cucujoidea are represented by primitive (*Parandrexis*) as well as advanced (*Praemordella* and *Jurallecula*) forms. The Chrysomeloidea are represented by the rather diverse Protoscelinae, considered to be phytophages. The total absence of Cerambycidae is noteworthy. Rhynchophora are particularly abundant in Karatau. They all belong to the newly established, primitive family Eobelidae which is exclusively Mesozoic. Eobelid fossils are slightly less numerous than click beetle fossils. They are very diverse; 30 species and 16 genera grouped into four subfamilies are described in this text.

The Karatau beetles are also ecologically very diverse. The Jurassic Lake of Karatau apparently had normal* salinity. Absolutely no aquatic insects lived in it; in any case no fossil larvae have been found. The adult
14 beetles (schizophoroids, gyrinids, coptoclavids, hydrophilids) fell into the lake during flight and died. The diversity of Coptoclavidae in Karatau may be emphasized once again; the number of genera found here is greater than in all the remaining sites. The Karatau period** apparently coincided with the maximum flourishing of this strictly Mesozoic, highly specialized family. The well-known Solenhofen site in the Federal Republic of Germany is second in the diversity of its coptoclavids; this site is almost coeval with Karatau. The littoral coastal beetles—to which many, if not all, Geadephaga and Staphylinidae belong—are fairly abundant in Karatau.

Terrestrial phytophagous beetles from Karatau are mainly associated with woody plants and are represented by xylophages, more accurately, by xylomycetophages. Distinctly phyllophagous forms are absent among them. Even the phytophagous Protoscelinae, judging from the mode of life of their closest extant relatives, inhabited pachycaulous sago palms (Cycadophyta) or Bennettitales. A large proportion of the dendrobionts were probably confined to conifer trunks. In any case, the abundance of cupedids in the

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*This is a correct translation of the Russian, but from the context it seems that the word "abnormal" may have been intended—Scientific Editor.

**We are not aware of any Karatau period. Since the reference is obviously to the Karatau site this sentence can be reworded as "The Karatau site apparently exhibits the greatest diversity of this strictly Mesozoic, highly specialized family"—General Editor.

Mesozoic correlates well with the abundance of conifers and with the level of carbon accumulation in predominantly conifer rich region. Cupedids were the most widely distributed of the Jurassic dendrobionts. They fed on wood partly decomposed by fungi. Possibly, only metallic wood borers fed on fresh wood. The remaining highly abundant Karatau Elateriformia were associated with wood highly decomposed by fungi. The ecology of the Eobelidae is of considerable interest. Their larvae probably lived in the ovules and strobilae of cycadoid gymnosperms, Cycadophyta and Bennettitales. The ecology of some present-day Oxycorynidae, as well as the correlation between the abundance of Eobelidae and that of the Cycadophyta, supports this assumption.

Coleopteran fossils from the dawn of the Early Cretaceous (Neocomian) are distributed rather unevenly. The fossils collected from the Upper Jurassic Baisa site in the Vitim plateau of Trans-Baikal far outnumber those from other sites, although over a hundred have already been collected from a single site in Trans-Baikal and Mongolia. Therefore, an attempt will be made to characterize the Early Cretaceous Coleoptera from this site, while those from the remaining sites will be introduced only as supplementary material. The sites yielding early Cretaceous insects are plentiful in Trans-Baikal, Mongolia and China. They are also found in the remaining territory of Siberia in Kazakhstan, but comparably rich sites have not yet been exposed. Isolated finds are known from western Europe, North Africa, South America and Australia.

In general features, the Neocomian beetle fauna is similar to that of the Late Jurassic. The Archostemata are somewhat less abundant but continue to play an important role, constituting a few percent of the collected fossils. Eight species belonging to 6 genera and 2 families of the Archostemata have been described. In some sites cupedids occur in unusually large numbers or even predominate. All these sites are poor in fossils, but cupedids turn out to be over represented. It may simply be that chance has favoured their selection from a fauna in which they actually constitute only a small percent. Among the Archostemata, cupedids predominate in all faunas. Of the remaining families of the Archostemata, the only representatives are the ademosynids. However, one cannot speak of these beetles with absolute certainty as of the Archostemata*. Judging from the elytral composition, schizophoroids still occurred in this period, but not a single well preserved fossil of these forms has been found. Among cupedids, the *Notocupes* predominates as usual; the exclusively Late Mesozoic genera are very rare, and so are the Cenozoic type of cupedids.

Fossil Adephaga are very abundant in most collections of Early Cretaceous beetles. This predominance is due to the vast collections of larvae of a single species of water beetle, *Coptoclava longipoda* Ping, which already exceed a thousand. However, even if we exclude this species, the Adephaga still numerically exceed the Archostemata.

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*Considering what has been said in the first part of this sentence the end part should read "... as of other members of the Archostemata"—General Editor.

To date, coptoclavids and whirligigs are the only aquatic Adephaga in the Lower Cretaceous sites. The examples of Coptoclavidae include: the most advanced, widespread, monotypic genus *Coptoclava*, from the Early Cretaceous of East Asia; and the most primitive *Necronectes*, represented by a single fossil from Brezina in North Africa. The whirligigs possess the typical Mesozoic facies. The Geadephaga are represented by ground beetles and trachypacheids. Both* genera of trachypacheids already existed in the Late Jurassic; the carabid genera [from the Lower Cretaceous sites**] were specific, but for the most part primitive, and not well differentiated from the Late Jurassic forms. Only one fossil may be related to the present-day carabids, but it is very incomplete. The discovery of an aquatic larva of *Cretotaenia* with the full complement of abdominal segments is noteworthy.

The Polyphaga are diverse and abundant, but possess a primarily Mesozoic appearance. Among the Staphyliniformia, rather diverse hydrophilids and staphylinids of the lower† subfamilies are found. Among the Eucinetiformia, Eucinetidae similar to present-day *Eucinetus* are encountered; they are definitely more abundant than others. The Scarabaeiformia are extensively represented for the first time in the Early Cretaceous. In the Lower Cretaceous deposits of East Asia, fossil Scarabaeidae are the most abundant among the terrestrial beetles. Compared to the Late Jurassic, their numbers rose more than tenfold. Despite their high diversity and excellent preservation, it is difficult to ascertain the taxonomic position of the Early Cretaceous Scarabaeidae. Its members are externally similar to the fairly advanced forms, often resembling May beetles. However the important structural features of this family, such as the form of the hind wings and spiracles, when evident, are found to be extremely primitive, and confirm their inclusion in the lowest Scarabaeidae‡, including the Geotrupidae which are presently considered a separate family.

Elateriformia, abundant in the Late Jurassic, become exceedingly rare in the Early Cretaceous. The metallic wood borers increase slightly in number, whereas the click beetles become distinctly fewer. The Protagrypninae lose their dominance among the click beetles, and the Oestodinae make their appearance (V.G. Dolin, personal communication). Also noteworthy is the first appearance of the Throscidae and Cerophytidae.

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*Since names of these genera have not been given above it is not certain that the author implied two instead of 'both'—General Editor.

**—Scientific Editor.

†More primitive—Scientific Editor.

‡So given in the Russian original. Should read Scarabaeidae (sensu lato)—General Editor.

The Cucujiformia were previously not as important as now. The Cucujoidea are represented by the Nitidulidae and Scraptiidae, essentially indistinguishable from present-day forms. The Chrysomelidae are and apparently still represented only by Protoscelinae. In the Baisa site, beetles externally similar to the primitive Cerambycidae have been found, but their incomplete preservation precludes their exact placement.

The Early Cretaceous Rhynchophora are diverse; even primitive belidoids are present which, according to L.V. Arnol'di may be directly related to Belidae and Oxycorynidae, but V.V. Zherikhin considers that they belong with Eobelidae. Also, representatives of the Attelabidae and Curculionidae are found for the first time. Ecologically, the Early Cretaceous beetles preserve the Mesozoic character. The aquatic beetles are represented by pleustonic predators (adult Coptoclavidae and Gyrinidae); nektonic predators (larvae of *Coptoclava*); and hydrophilids, which are decidedly phytophagous in the adult stage. The latter, despite their general resemblance to *Spercheus*, were not adapted to the pleustonic mode of existence, and probably fed mainly on charophytic algae while moving among submerged vegetation.

Terrestrial predators are represented by staphylinids, carabids and trachypacheids of Mesozoic appearance, which were evidently dwelling near water. It is even possible that the aquatic caraboid larvae of *Cretotaenia* belonged to the trachypacheids.

Among the abundant Scarabaeidae, probably there were no forms similar in mode of life to the modern, cosmopolitan dung beetles and May beetles; instead, they were probably mycetophages and carrion-feeders. A large proportion of the beetles in the Early Cretaceous as well as the Late Jurassic were xylobiontic phytophages associated with wood more or less decomposed by fungi. As usual, phyllophages were few or absent among the
16 beetles. Among weevils there are forms obviously associated with angiosperms; they are still very rare, but their remains have been found in these deposits (Bakhrameev, 1973).

The insect composition of the Early Cretaceous is quite unique. An extensive proliferation of angiosperms occurred during this period and, apparently linked with this, a change in the composition of the entomofauna. The majority of the Late Mesozoic forms characteristic of the end of the Jurassic and beginning of the Cretaceous disappear; they were quite unexpectedly replaced, not by Cenozoic forms, but by the Late Mesozoic forms not found earlier in taphocenoses and considered totally extinct. Unfortunately, we do not have rich, well-preserved fossils of large beetles from the Aptian and Albian stages. They are either small or fragmentary and cannot be accurately identified. In the Trans-Baikal sites, whose age was determined as the end of the Early Cretaceous, fossils of Liadytidae have been found which were previously encountered only in the first half of the Jurassic.

Trachypacheidae and Hydrophilidae very near the Early Jurassic forms were also found at these sites. Finally, from the Middle Cretaceous deposits of the Labrador Peninsula, a beetle has been found which was described as a member of the monotypic family Labradorocoleidae. This family may be related exclusively to beetles of the family Tshekardocoleidae which are characteristic of the Early Permian and, even in the Late Permian, so far only one specimen has been found (Ponomarenko, 1969a). Based on elytral composition, this site resembles the Early Jurassic; schizophoroid type elytra, not observed in younger deposits, predominate. Apparently, relict forms occurred in the new biocenoses; the forms typical of relatively stable Mesozoic and Cenozoic biocenoses began to disappear while new relatively stable cenoses with typical Cenozoic groups had not yet fully formed.

The insects of the Late Cretaceous can be studied far better than those of any other period. We have not only sites with the imprints of the Late Cretaceous insects but also numerous sites with insect remains embedded in fossil resins, providing a good sequence of forms through the entire Late Cretaceous. The study of these collections has just begun and it is possible to present only the first tentative results.

Cenozoic forms predominate among the Late Cretaceous insects, just as angiosperms do among the Late Cretaceous plants. The Mesophyte-Cenophyte boundary also delineates one of the greatest changes in the evolution of beetles. The composition of the Late Cretaceous beetle fauna is essentially Cenozoic. It is true that the abundance of Archostemata, particularly cupedids, does not decrease; in Siberia their numbers even increase. This may have been linked to the extinction of chekans, while conifers retained their importance. In the late Cretaceous, cupedids were the only Archostemata, represented by the very widespread Mesozoic genus *Notocupes* and the rarely encountered examples of present-day *Omma* and *Tetraphalerus.*

Strictly Mesozoic forms are totally absent from the Late Cretaceous Adephaga. Dytiscidae, Gyrinidae and Carabidae of the present-day type are found here, while advanced forms such as Harpalinae* are already present in the first half of the Late Cretaceous. Most of the subfamilies and tribes of extant Adephaga had apparently already evolved in the Late Cretaceous.

A similar picture is seen for the Late Cretaceous Polyphaga which have been almost totally excluded from the investigation. All these are closely related to the Cenozoic forms; strictly Mesozoic groups are either completely absent (Eobelidae and Protoscelinae) or are very rare (Protagrypninae). Unfortunately, it is not yet known whether phyllophages were present among the Late Cretaceous beetles, but Cenozoic longhorned beetles and metallic wood borers were undoubtedly more common than in the Early Cretaceous.

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*Family Carabidae—Scientific Editor.

In conclusion, it may be said that two major faunal changes occurred in the evolution of Coleoptera during the Mesozoic: the first between the Early and Late Jurassic when the Archostemata lost their dominance, and the second at the end of the Early Cretaceous when the Mesozoic fauna was replaced by the Cenozoic.

Descriptions of New Taxa

[In order to present measurements in a format which will be more familiar to most of our readers, Russian expressions such as "*A* twice shorter than *B*" have been translated as either "*A* half as long as *B*" or "*B* twice as long as *A*". Decimals have been transformed into fractions when convenient—Scientific Editor.]

SUBORDER ADEPHAGA

17 **Family TRIAPLIDAE Ponomarenko, Fam. Nov.**

Diagnosis. Fairly large, elongate, cylindrical beetles with head bent ventrally. Head small, ortho- or opisthognathous. Antennae weakly moniliform. Prothorax with distinct sternopleural and notopleural sutures. Forecoxae protuberant, not separated by intercoxal process. Mesosternum short, mesopleuron small. Suture dividing mesothoracic postepisternum distinct. Middle coxae converging. Metasternum roundly tapering anteriorly; metepisternum extending to middle coxal cavities; transverse metasternal suture distinct. Hind coxae fully separating metasternum and abdomen, long, with large femoral plates covering basal abdominal sternites. Abdomen with six visible sternites, the first small, and last noticeably longer than the remaining. Elytra without punctate striae, with a projection situated laterally on inner side*.

Composition. Single genus in the Triassic of Soviet Central Asia.

Comparison. Differs from other families, except Haliplidae, in the structure of hind coxae and abdominal base; differs from Haliplidae in ventrally bent head, contiguous forecoxae without intercoxal process, metepisterna extending to middle coxal cavities, and shorter hind coxae with smaller femoral plates.

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*The relevant figures suggest the following interpretation of the preceding phrase: "with a *projection* [= ridge or shelf] situated *laterally* [= toward the costal margin] on *inner side* [= the inflexed portion of elytron, the elytral epipleuron]."—Scientific Editor.

Genus *Triaplus* * Ponomarenko, gen. nov.

Species name coined from Triassic, and genus *Haliplus*.

Type species. T. macroplatus sp. nov.; Triassic of Soviet Central Asia.

Description. Body elongate, teardrop-shaped, posteriorly tapering. Head short, strongly transverse, retracted under pronotum, often entirely concealed. Antennae fairly long, slender: basal segments cylindrical, distal markedly moniliform. Pronotum transverse, forming semi-circular hood above the head. Prosternum rectangular, shorter than forecoxae. Propleura not at all narrowing anteriorly. Mesosternum much shorter than middle coxae. Middle coxae rounded. Metasternum transverse, strongly and roundly tapering anteriorly, its hind margin and transverse suture nearly straight. Hind coxae slightly shorter than broad, laterally deeply incised with the portion extending backward along the midline almost at right angles to the coxal base. Femoral plates approximately as long as wide. Abdomen markedly longer than the meso- and metasternum together, last sternite much longer than the penultimate. Elytra long, extended, pointed apically with distinct inner projection** approximately level with hind coxae. Body with large and dense punctures.

Species composition. Two species in the Triassic of Soviet Central Asia.

18 *Triaplus macroplatus* Ponomarenko, sp. nov.
(Plate I, Photos 1, 2; Figure 1)

Species name coined from 'macros' (Greek)—large, and 'plata' (Greek)—plate.

Holotype. No. 2971/104, PIN, impression of beetle without antennae, legs and abdomen, Soviet Central Asia, Southern Fergana, Kirgiz SSR, Osh Oblast, Batken region, Madygen area (Madygen site, south-western part). Triassic, Madygen series.

Material. Besides holotype, three impressions of beetles, Nos. 2083/163, 2905/24 and 2971/111, from the same site.

Description. Prosternum slightly shorter than forecoxae; propleuron narrow, elongate. Forecoxae equal in length and width, mesally protuberant. Mesosternum one-third length of middle coxae. Middle coxae somewhat transverse. Metepisternum strongly broadened anteriorly. Femoral plates together forming an almost perfect semicircle. True abdominal sternites III–VI equal in length, half the length of the last. Legs short, femora uniformly thickened, tibiae widening from base to apex. Inter-puncture distance on dorsal surface of body nearly equal to (diameter of) punctures themselves, punctures much smaller on ventral surface. Punctures on all ventral sclerites identical.

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*Given as Triaplidae in the Russian original—General Editor.

**See note on page 19—Scientific Editor.

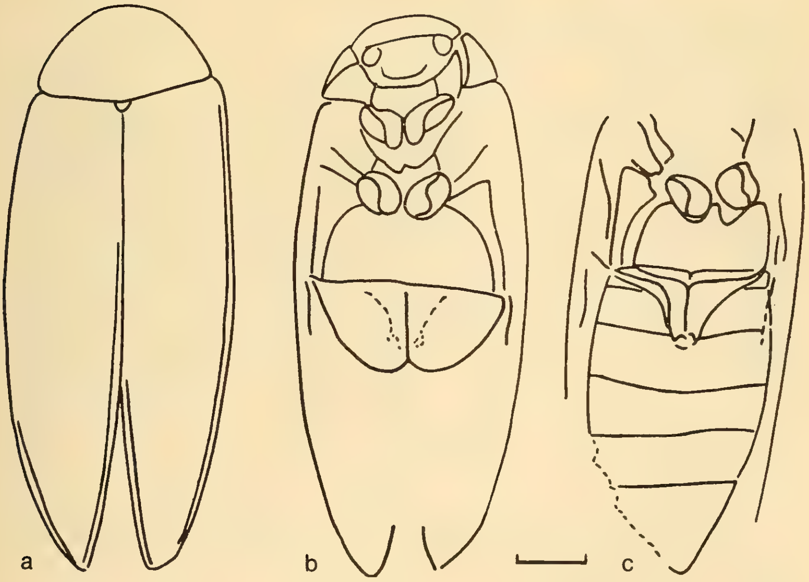
Dimensions. Body length about 7–8 mm, width 2.9–3.3 mm, elytral length 6.5–7.0 mm.

Comparison. Distinguished by longer forecoxae and shape of femoral plates together forming an almost perfect semicircle.

Triaplus laticoxa Ponomarenko, sp. nov.
(Plate I, Photo 3; Figure 2)

Species name coined from 'latus' (Latin)—wide, and 'coxa' (Latin)—pelvis.

Holotype. No. 2240/179, PIN, impression of almost entire beetle, shape of the impression slightly obliterated by postfossilization expansion of the
19 rock. Soviet Central Asia, Southern Fergana, Kirgiz SSR, Osh Oblast, Batken region, Madygen area (Dzhailyaucho site, northern part). Triassic, Madygen series.



18 Fig. 1. *Triaplus macroplatus* sp. nov. a, b—holotype PIN No. 2971/104: a—dorsal view; b—ventral view; c—paratype PIN No. 2905/24. Madygen, Triassic. Here and in the following figures the linear scale is approximately 1 mm.

Material. Besides holotype, seven almost entire impressions of beetles, Nos. 2069/1228, 2069/1294, 2070/1887, 2240/216, 2240/218, 2240/243, 2555/1720, from the same site. Fossils of beetles rather highly variable in size and possibly belong to more than one species. However, structurally very similar, but a comparison of the proportions of individual sclerites is very difficult due to obliteration associated with expansion of the embedding rock.

Description. Length of head half its width. Prosternum slightly shorter than forecoxae, propleuron of subequal length and width. Forecoxae somewhat transverse. Mesosternum half the length of middle coxae, middle coxae equal in length and width. Metepisternum strongly broadening anteriorly, narrowing at posterior margin. Femoral plates somewhat broadening from base posteriorly, and rounded only just before apex. Abdominal sternites III–VI equal in length, half the length of the last, the seventh. Legs short, hind femora slightly clavate, broadest in basal third. Body dorsally with tubercles and uniform punctures, ventrally with large dense punctation, punctures on metasternum and femoral plates particularly large.

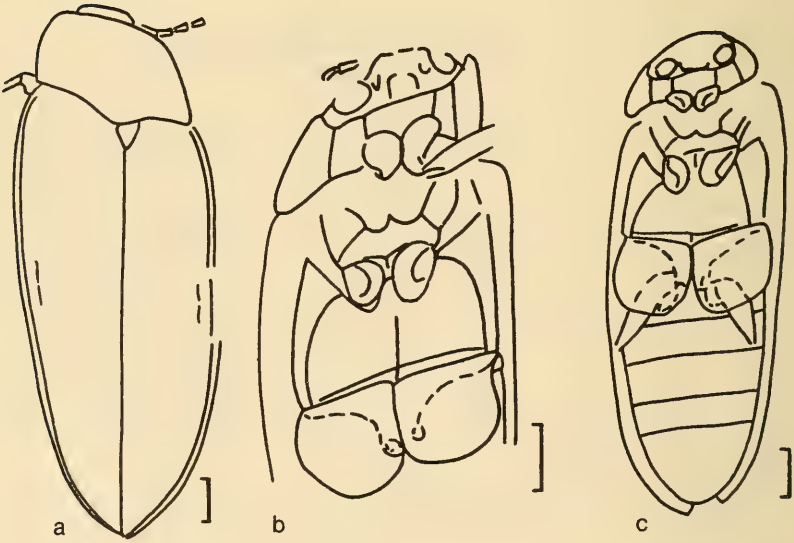


Fig. 2. *Triaplus laticoxa* sp. nov. a, b—holotype PIN No. 2240/179: a—dorsal view, b—ventral view of head and thorax; c—paratype PIN No. 2555/1720. Dzhailyaucho, Triassic.

Dimensions. Body length 11–14 mm, width 3.5–4.0 mm, elytral length 10.0–11.5 mm.

Comparison. Distinguished by longer prosternum, and femoral plates broadening posteriorly from base, extending along the middle coxae*.

INFRAORDER HYDRADEPHAGA

SUPERFAMILY DYTISCOIDEA LEACH, 1815

Family PARAHYGROBIIDAE Ponomarenko, Fam. Nov.

Diagnosis. Water beetles. Larvae nektonic, with natatorial legs and urogomphi. Head sessile, rectangular, with roundish projecting nasale. Antennae 20 four segmented, nearly as long as head. Mandibles short, strongly curved, with pointed elongate apices and wide base, mesal surface with small denticles (retinaculae). Prothorax somewhat longer than other body segments which are each of nearly equal length. Abdomen eight segmented; last tergite somewhat prolonged posteriorly at middle, overlapping the only functional pair of spiracles. All 3 pairs of legs similar, bearing sparse stiff bristles. Urogomphi long, distinctly segmented, with apical bristles.

Composition. Single genus from the Jurassic of Trans-Baikal.

Comparison. Most closely resembles the Hygrobiidae in the structure of head and legs, but differs from it in the structure of mandibles and retention of the eighth abdominal segment; it differs from most dytiscoids by the presence of retinaculum, and from the forms with retinaculum by the shape of head and natatorial legs, long urogomphi, and short eighth abdominal segment; from the Coptoclavidae it differs in the shape of mandibles and in possessing stiffer and sparser bristles on uniformly wide leg segments.

Remarks. Description of the new family is based almost exclusively on plesiomorphic characters of water beetles. Thus affinity of *Parahygrobia* with any family of water beetles is based on symplesiomorphy. *Parahygrobia* does not have features which allow it to be considered an ancestor of water beetles; it is highly unlikely that such benthic phytophages as the Noteridae originated from them.

Genus *Parahygrobia* Ponomarenko, gen. nov.

Species name coined from the genus *Hygrobia.*

Type species. P. natans sp. nov.; Jurassic of Trans-Baikal.

Description. Small larva, robust with rather long legs and urogomphi. Head almost square, slightly broadening anteriorly. Nasale small, length

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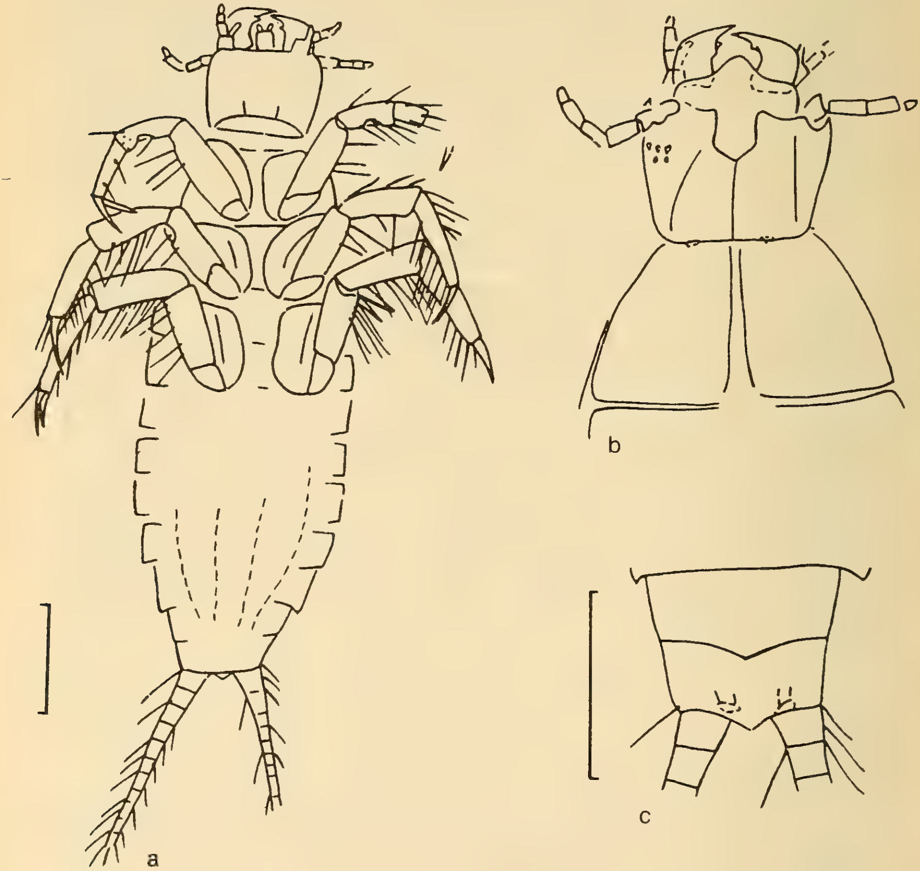
*As given in the Russian original, but presumably the *hind* coxae are the structures indicated here—Scientific Editor.

much less than width, its demarcation distinct basally at middle. “Epicranial suture” Y-shaped, its stem longer than fork. Length of antennal segments less than double the width. Pronotum narrowed anteriorly. Eighth abdominal segment slightly shorter than the preceding; tip of seventh tergite angularly projecting posteriorly. Urogomphi slightly shorter than the abdomen, noticeably narrowing apically, urogomphal hairs longer than the segments. Legs long; femora and tibiae slightly thickened, tarsi virgate; femora, tibiae and tarsi with long natatory bristles, their length slightly less than that of the distal leg segments. Claws large, their bases broad, not narrower than the tip of tibia, only half the length of tarsus.

Species composition. Monotypic genus.



21 Fig. 3. *Parahygrobia natans* sp. nov. Holotype PIN No. 3053/423: a—ventral view, b—dorsal view of head and prothorax, c—tip of abdomen. Uda, Jurassic.

Parahygrobia natans Ponomarenko, sp. nov.
(Plate I, Photo 4; Figure 3)

Species name coined from ‘natans’ (Latin)—natatory.

Holotype. No. 3053/423, PIN, impression of entire larva. Trans-Baikal, Buryat ASSR, Eravninsk region, River Uda close to Ulan-Mailo settlement (Uda site): Jurassic, Uda series.

Description. Central part of nasale occupying nearly one-third its width, apically rounded (Fig. 3b). Epicranial suture bifurcated midlength of the head, its branches initially diverge, then run parallel almost to the anterior margin of the head, near which they again sharply diverge laterally. Lateral ocelli on a single sclerite*, separated by more than their diameter. Antennae slightly shorter than the head, first segment shorter, fourth longer than the subequal second and third segments. Mandibles slightly longer than wide, retinaculum blunt and small in the apical third. Three proximal segments of maxillary palps nearly equal, the terminal segment noticeably thinner than the proximal ones.

21 Pronotum almost equal to the head in length and to its width anteriorly, anterior pronotal margin nearly half the width of posterior margin. Meso- and metathorax each two-thirds the length of prothorax. All abdominal segments of nearly equal length, eighth slightly shorter than the remaining segments. Width of the widest (fourth abdominal) segment twice the width of eighth at base. Urogomphi three-fourths the length of abdomen, distinctly 10-segmented. Legs only slightly shorter than body. Coxae large, oval, with distinct longitudinal ridge, slightly shorter than femur. Trochanters single, one-fourth the length of femur. Forefemora uniformly convex at middle, one-and-a-half times longer than tibiae and tarsi, each bearing three bristles on the posterior margin. Foretibiae with a pre-apical notch, claws of foretarsi straight, slightly shorter than tarsi. Bristles on foretibiae and tarsi denser on the posterior margin than on the anterior margin. Middle tibiae and femora equal, slightly shorter than tarsi; claws half as long as tarsi. Femora with a few bristles borne preapically on the posterior margin. Tibiae and tarsi with 5–7 bristles on the anterior and posterior margins. Hind femora and tibiae longer than middle ones, equal to each other, distinctly shorter than tarsi. [Tarsal] claws unequal: larger claw half the tarsal length, straight; shorter claw thicker and curved.

Dimensions. Length of larva 5.8–6.5 mm, length of head 0.8–1.0 mm, length of foretarsus 0.4–0.5 mm, midtarsus 0.5–0.6 mm, length of urogomphi 1.4–1.5 mm.

Remarks. Sediments with *Parahygrobia* larvae are considered Upper Jurassic (Skoblo, 1968), but some larvae of aquatic insects collected here cannot be distinguished from those of the Middle Jurassic on the basis of the described characters. Hence the problem of their precise age remains unresolved (for greater details see Rasnitsyn, 1975).

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*The Russian original uses the term ‘apodeme’ which has been changed to sclerite—Technical Editor.

Family COPTOCLAVIDAE Ponomarenko, 1961

22 Coptoclavidae Ponomarenko, 1961, p. 68; Rohdendorf and Ponomarenko, 1962, p. 225; Ponomarenko, 1975, p. 123.

Diagnosis. Large, rarely medium-sized, aquatic beetles. Head with two pairs of eyes, dorsal and ventral. Metepisternum not reaching middle coxae, hind coxae not broadening anteriorly, transverse metasternal suture absent. Middle and hind legs natatory, tibiae broadened, together with tarsi forming an oar-like lobe.

Larvae nektonic, actively natatory, with cylindrical body not tapering posteriorly, and with long urogomphi. Mandibles with denticles on mesal surface. Forelegs raptorial, with spines; middle and hind legs natatory, with thickened tibiae and tarsi, bearing slender and dense natatory hairs. Abdomen 8-segmented, spiracles metapneustic, urogomphi with fused segments.

Composition. Three subfamilies: Necronectinae in the Jurassic of Europe and Asia, and in the Early Cretaceous of Africa; Charonoscaphinae in the Jurassic of Asia, and Coptoclavinae in the Early Cretaceous of East Asia.

Comparison. Distinguished from all natatory beetles as a four-eyed form with natatory middle and hind legs, and hind coxae not anteriorly broadening; from whirligigs distinguished by long legs and dominance of metathorax over mesothorax.

Subfamily Necronectinae Ponomarenko, Subfam. Nov.

Diagnosis. Large beetles. Hind coxae with small femoral plates. Hind tibiae and tarsi long and slender without any broadening, and with long, slender, natatory hairs.

Composition. Genus *Necronectes* found in the Middle Jurassic of Trans-Baikal, Late Jurassic of South Kazakhstan and Early Cretaceous of Algeria; genus *Exedia* in the Late Jurassic of South Kazakhstan; genus *Pseudohydrophilus* in the Late Jurassic of Western Europe. Aquatic larva of *Stygeonectes* from the Middle and possibly Late Jurassic Baikal is tentatively placed here.

Comparison. Distinguished from the remaining subfamilies by slender hind tibiae and tarsi in adults and by femoral plates on hind coxae. The *Stygeonectes* larvae are distinguished from the *Coptoclava* larvae by the single denticle on the mesal surface of the mandible and by the proportions of leg segments.

Genus *Necronectes* Ponomarenko, gen. nov.

Species name coined from 'necros' (Greek)—dead, and 'nectes' (Greek)—oarsman.

Type species. N. aquaticus sp. nov. Middle Jurassic of Baikal.

Description. Large beetles with rather elongate body expanded at shoulders. Head and pronotum relatively small. Head transverse, strongly retracted into the anterior emargination of the prothorax. Pronotum expanded in front of posterior angles. Mesothorax only slightly smaller than metathorax, metapleura larger than mesopleura. Metepisterna broadening slightly anteriorly their inner margins almost without a curve; anteriorly not reaching middle coxal cavities. Transverse metasternal suture faint or not noticeable. Femoral plates scarcely longer than and about three times as wide as hind coxae, strongly tapered laterally. Elytra smooth. All legs with natatory hairs. Fore- and middle tarsi broadening, their proximal segment long, broadening apically, second and third transverse, notched apically, last segment virgate.

Species composition. N. aquaticus from the Middle Jurassic of Baikal (Ust'-Balei), and *N. giganteus* from the Upper Jurassic of south Kazakhstan (Karatau). The incomplete fossils from the Early Cretaceous of Algeria and the Jurassic of Soviet Central Asia are included in this genus.

Comparison. Distinguished from other genera by basally expanded pronotum.

23 *Necronectes aquaticus* Ponomarenko, sp. nov.

(Plate I, Photo 5; Figure 4)

Species name coined from 'aquaticus' (Latin)—aquatic.

Holotype. No. 722/23, PIN, almost entire impression beetle. Baikal, Irkutsk, Oblast, Irkutsk region, right bank of river Angara, below Ust'-Balei village (Ust'-Balei site). Lower strata of the Middle Jurassic, Cheremkhovsk series.

Material. Besides the holotype, one poorly preserved impression of a male and part of an isolated elytron, specimen Nos. 2363/15 and 2363/17 from Khudoga site (Buryat ASSR, Dzhidin region, Dzhida river basin, waterdivide of Khudoga and Simkhak rivers, Ichetui series). The impression of the beetle differs somewhat from the holotype in the shape of body and of fore femora, but resembles the holotype in most other characters.

Description. Body convex, oval, flattened dorsally, with medium keel ventrally. Head and pronotum together small, approximately one-sixth the body length. Length of head almost half the occipital width, narrowing anteriorly. Dorsal eyes small, almost one-fourth the length of head, separated by more than their diameter. Ventral eyes on each side of head, situated anterior to dorsal ones, elongate. Gular plate short and wide, almost square, mental sections almost equal. Antennae slender, filiform, longer than the head and prothorax together, segments cylindrical, only scape noticeably broadening apically, two apical segments shorter than the rest.

Length of prothorax one-third its width, widest in the anterior third, its lateral margin with a depression in front of posterior angles. Pronotal angles rounded, anterior margin not emarginate, concealing the base of the head dorsally. Pleura* wide, narrowing anteriorly. Prosternum projecting roof-like**, shorter than forecoxae and prosternal process. Mesosternum small, bordering middle anteriorly, laterally strongly tapered, with shallow notch in middle. Mesopleuron almost square, twice as long as mesosternum, suture between mesepisternum and mesepimeron dividing the pleuron into equal triangular parts. Mesepimeron extending to middle coxal cavities only as narrow tongue. Metathorax transverse; width of metasternum more than twice the distance between middle and hind coxae, its lateral margins almost straight, hind margin angularly projecting backward. Transverse metasternal suture bent backward, weak. Longitudinal metasternal lines, corresponding to internal ridges, run from middle coxae backward and from hind coxae forward. Metepisternum triangular, its anterior margin half the length; [much longer than†] distance between inner corners of metepisternum and middle coxae much less than the length of anterior margin of metepisternum. Length of hind coxae with femoral plates half the width. Portion of hind coxae projecting over the abdomen almost one-third length of entire coxa. Femoral plates transverse, sharply tapered in lateral third.

Abdominal sternites subequal in length; only the last (seventh) slightly longer and in males with a shallow, wide, apical notch [exposing an additional sternite]. Eighth‡ sternite [of male] paired, irregular oval, with a flattened medial side and notched antero-lateral margin. Spiracles of seventh and eighth segments each one-third the length of seventh sternite, almost twice as large as the preceding spiracles. Parameres†† almost symmetrical, triangular, only slightly longer than wide.

Elytra smooth, epipleuron narrow, a long ridge present near lateral [= costal?] margin at middle third of elytron on lower surface. Forecoxae slightly projecting, almost round, length of trochanter nearly one-third length

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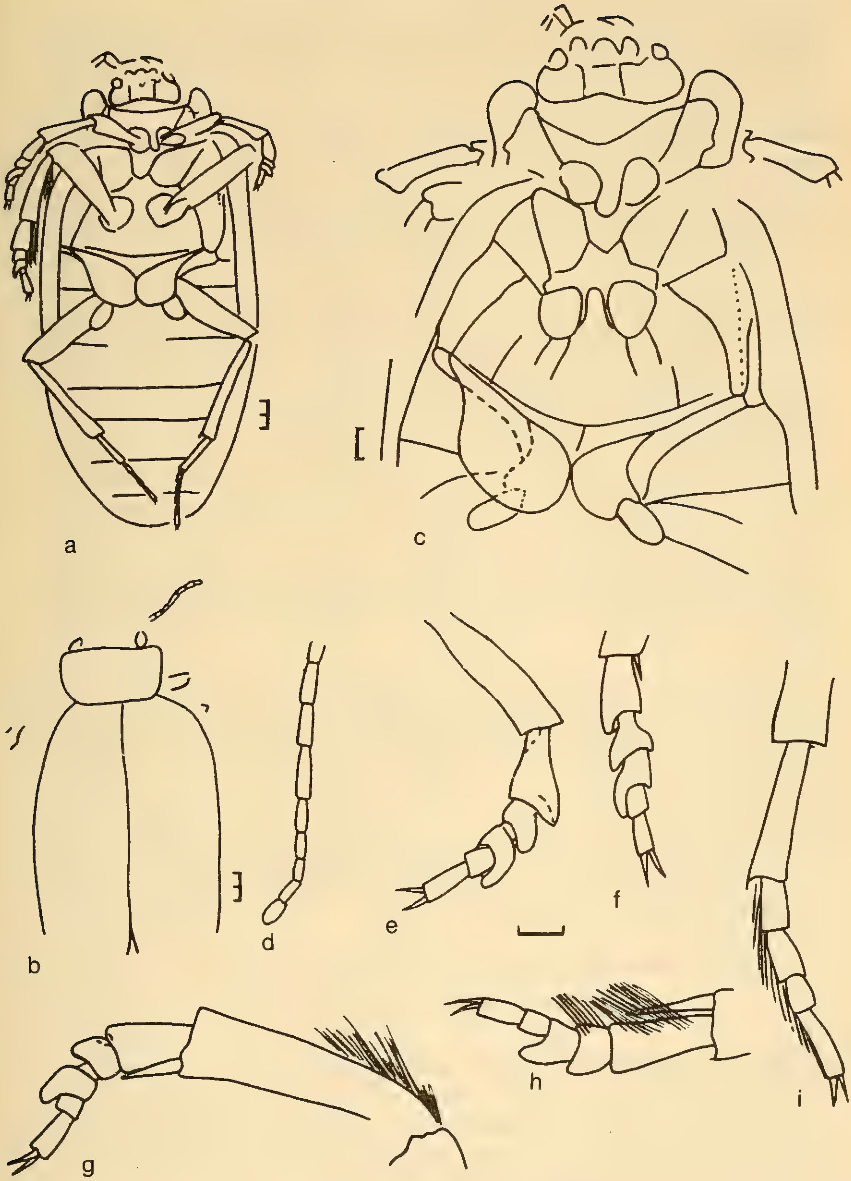
*The nature of description suggests the reference to the propleuron. If accepted, 'pleura' should be changed to 'propleura'—General Editor.

**Presumably the transverse anterior portion for the prosternum, minus its intercoxal process is referred to here—Scientific Editor.

†As in the Russian original but with brackets added. Deleting the bracketed phrase will restore meaning—Scientific Editor.

‡As in the Russsian original but contradicts the earlier statement—General Editor. This contradiction is eliminated with the addition of the bracketed interpolative remarks—Scientific Editor.

††Given as parameters in the Russian original—General Editor.



24 Fig. 4. *Necronectes aquaticus* sp. nov. Holotype PIN No. 722/23: a—ventral view, b—dorsal view, c—ventral view of head and thorax, d—antenna, e, f—forelegs, g, h—midlegs, i—hind legs.*

* Only one hind leg shown—General Editor.

of femur. Tibia slightly shorter than femur, flattened and curved, slightly broadening apically. Tarsi subequal in length, length of the first segment almost equal to the next three; second and third broadened, with apical notch, third segment articulating with the notch of second; fourth segment small,
24 almost square, fitting into notch of third; fifth twice as long as the preceding. Spur of foretibia shorter than first tarsal segment.

Middle femora one-third longer than forefemora. Tibiae two-thirds length of femora, flattened, apically broadening, their lateral margin serrate. Middle tarsus three-fourths the length of tibia; its first segment only slightly shorter than remaining segment together, twice as long as its apical width; second and third transverse, third with deep apical notch; fourth and fifth narrow, fourth a little longer, fifth twice as long as wide. Claws two-thirds the length of apical tarsal segment. Tibia and tarsus with median groove bearing long and dense natatory hairs.

Hind trochanters one-third the length of femora. Femora uniformly slightly thickened, hind femora as long as middle femora. Tibiae markedly
25 longer than femora, broadening apically and somewhat curving externally. Tarsi noticeably shorter than tibiae, their segments elongate, slightly broadening apically; first tarsal segment equal in length to three apical segments together, three times longer than second; second and third segments equal; fourth two-thirds of third; fifth almost equal to two preceding ones together.

Body with dense shallow punctures dorsally, almost forming transverse striae on elytra; smooth ventrally except for a few rather small punctures on the sternum. First and second visible abdominal sternites with large circular punctures laterally.

Dimensions. Body length 34–35 mm, width 15 mm, elytral length 25 mm.

Comparison. Distinguished by the very small head and pronotum, long, drawn-out body, and fine punctures on elytra.

Necronectes gigas Ponomarenko, sp. nov.
(Plate I, Photo 6, Figure 5)

Species name coined from 'gigas' (Latin)—gigantic.

Holotype. No. 2554/477, PIN, beetle with incompletely preserved legs. South Kazakhstan, Chimkent Oblast, Alagabass region, south-western flank of Kashkarata river valley, Aulie area in Mikhailovka village (Karatau-Mikhailovka site); Upper Jurassic, Karabastau series.

Description. Large beetle with oval, flattened body. Head and pronotum together about one-fourth of body length. Length of head two-thirds its width. Dorsal eyes rather large, round, distance between ocular sclerites* less than

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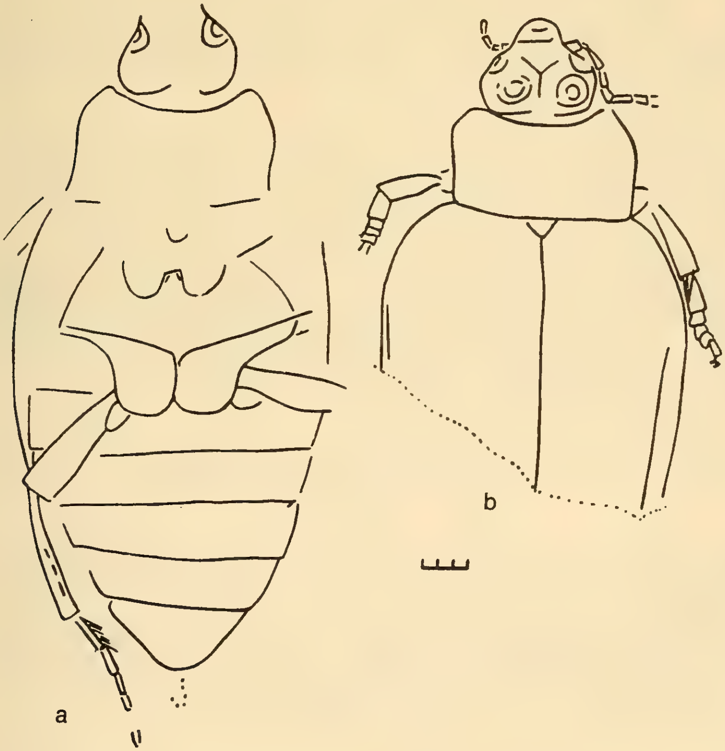
*See our note on page 25—General Editor.

their diameter. Ventral eyes round, placed laterally on head in front of dorsal ones. Antenna short, filiform, not reaching the base of pronotum, its segments noticeably broadening apically; scape cylindrical, short, third segment a little longer than others.

Length of prothorax half its maximum width just before middle. Pronotum narrowed anteriorly, roundly emarginate at anterior margin, expanded in front of posterior angles. Mesosternum small, with distinct depression for prosternal process. Mesopleura almost square, pleural suture dividing them into equal triangular parts. Metasternum four times wider than distance between middle and hind coxae. Metepisternum rather wide posteriorly, anteriorly wider than at posterior margin, almost double; middle coxae separated from inner corners of metepisternum by half the length of latter at anterior margin. Length of hind coxae two-fifths the width; portion of coxa projecting over abdomen longer than wide, its length half the width of entire coxa. Femoral plates almost square, two-fifths the coxal width,



26 Fig. 5. *Necronectes gigas* sp. nov. Holotype PIN No. 2554/477: a—ventral view, b—dorsal view. Karatau, Upper Jurassic.

sharply tapering laterally, their notches almost rectangular. Abdomen posteriorly strongly narrowing, almost pointed at apex, last sternite triangular, first visible and third to fifth sternites equal in length, last longer but second longest.

Elytra smooth, epipleuron narrow, a long ridge present near lateral [= costal?] margin at middle third of elytron. Forefemora thickened; tibiae much shorter than femora and uniformly broadening to apex. Tarsi equal in length to tibiae. First tarsal segment triangular, longer than the three following together; second to fourth transverse, slightly broadened apically, weakly notched at apex. Last segment slightly narrower than preceding segments. Middle tibiae longer than foretibiae, two-thirds the length of middle femora, tarsus slightly shorter than tibia, first segment slightly broadening from base to apex, scarcely longer than the three following segments together; second to fourth segments transverse, weakly notched apically. Last segment slightly longer than preceding segment. Spur of middle tibia not extending to apex of first tarsal segment. Hind femora not longer than middle femora, equal to tibiae. Hind tibiae slightly broadening apically, flattened, with a groove bearing natatory hairs. Tarsus noticeably shorter than tibia, its first segment one-and-a-half times longer than the subequal second and third segments. Tarsal segments slender, cylindrical.

Body dorsally with dense punctures, finer on head and pronotum, coarser on elytra. Large punctures of elytra fused into intermingling transverse striae. Punctures small and sparse ventrally. First abdominal sternite with large circular punctures on each side of femoral plates.

Dimensions. Body length 48 mm, width 23 mm; elytral length 33 mm.

Comparison. Distinguished from *N. aquaticus* sp. nov. by large head and pronotum and posteriorly strongly tapering abdomen, from *N. cyrenaicus* sp. nov., by narrow, laterally highly tapering femoral plates and from *N. planus* sp. nov. by transverse hind coxae.

Material. Holotype.

Necronectes cyrenaicus Ponomarenko, sp. nov.
(Plate I, Photo 7; Figure 6)

Species name coined from 'Cyrenaica' (Latin)—Roman province in North Africa.

Holotype. No. 3394/24, PIN, metathorax, abdomen and elytra of beetle. North Africa, Algeria, Saida department, 20 km from Brezina settlement. Lower Cretaceous, Goteriv*? intermediate sandstone stratum.

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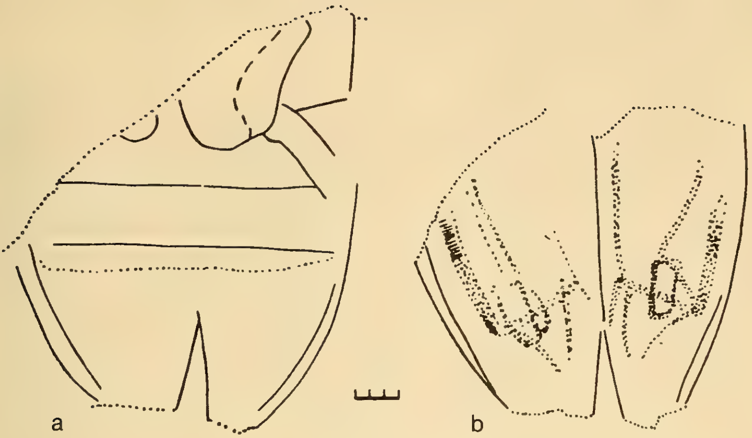
*Only here and on page 82 Goteriv is spelt with double 't' elsewhere it is with one 't', hence the preference—General Editor.



27 Fig. 6. *Necronectes cyrenaicus*, sp. nov. Holotype PIN No. 3394/24: a—ventral view of abdomen and tibia*, b—apices of elytra and folded wings. Algeria, Brezina, Lower Cretaceous.

Description. Large, oval, flattened beetle. Inner face of elytra in anterior third, with a long projection next to lateral margin. Epipleuron narrow. [Hind] wing with "oblongum" cell narrow, its medial width two-fifths its length. Length of hind coxae half their width; portion of coxa projecting over abdomen two-fifths width of entire coxa. Femoral plate transverse, tapering gradually in lateral third, lateral notch rounded, shallow. Second abdominal sternite one-and-a-half times longer than third. Abdomen strongly narrowing posteriorly to pointed apex. Elytra with coarse, large, sparse punctures, fusing into transverse striae and forming longitudinal rows along tracheae. Ab-
27 dominal sternites with fine, frequently contiguous punctures; punctures noticeably larger laterally on first visible and second abdominal sternites.

Dimensions. Body length about 45 mm, width 24 mm, elytral length about 35 mm.

Material. Holotype.

Comparison. Distinguished from *N. aquaticus* sp. nov. by posteriorly strongly tapering body, and from *N. gigas* sp. nov. by broad femoral plates.

Necronectes latus Ponomarenko, sp. nov.

(Plate I, Photo 8; Figure 7)

Species name coined from 'latus' (Latin)—wide or broad.

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*Tibia is seen to occupy the position of femur—General Editor.

Holotype. No. 3073/151, PIN impression of the thorax, abdomen and elytra of beetle. Soviet Central Asia, Kirghiz SSR, Batken region, Sagul Ravine (Shurab-III site). Jurassic.

Material. Holotype.

Description. Mesosternum very short, mesopleuron almost square, mesepisternum and mesepimeron rectangular, equal in length. Mesepimera wide, forming a part of the wall of middle coxal cavities. Metasternum almost three times wider than distance between rounded middle and hind coxae, strongly narrowing anteriorly, posterior margin angularly projecting backward. Transverse metasternal suture not visible. Metepisternum anteriorly broadening; width of anterior margin almost one-third the length. Length of hind coxae with femoral plates noticeably less than width; femoral plates strongly tapering laterally, transformed beyond middle of coxae into a narrow tongue running along the anterior coxal margin but not quite reaching its lateral corners. Last abdominal sternite twice as long as the remaining
28 equal sternites, its width two-thirds the width of abdominal base, apex blunt, rounded. All spiracles almost uniform in size. Elytra broad, flattened, sharply narrowing pre-apically. Epipleuron narrow. Integument of body very thin, wings and abdominal spiracles visible through it. Only coxal apices and margins of the last three abdominal sternites are sclerotized and pigmented. Elytra almost smooth, body with fine and sparse punctation ventrally, distance between punctures larger than the punctures themselves.

Dimensions. Body length about 15 mm, width 6.4 mm; elytral length 11.5 mm.

Comparison. Differs sharply from other species of the genus by broad abdominal apex, highly oblique hind coxae and laterally sharply tapering femoral plates. Probably merits separation into an independent genus, but its imperfect preservation prevents its full comparison.

Genus *Exedia* Ponomarenko, gen. nov.

Genus name coined from 'exedia' (Greek)—float.

Type species. E. plana. Upper Jurassic of South Kazakhstan.

Description. Large beetles with flat, oval body. Head large, transverse, dorsal eyes convergent. Pronotum rather strongly, roundly tapering anteriorly, emarginate in front. Metepisterna almost reaching middle coxal cavities. Posterior abdominal sternites shorter than preceding [anterior] ones. Forecoxae short, tibiae shorter than femora. Hind tibiae flattened, narrow, slightly curved. Elytra with raised ridges.

Special composition. Monotypic genus.

Comparison. Distinguished from other gnera by ridged elytra; in addition, differs from *Necronectes* in having pronotum not expanded at base and from *Pseudohydrophilus* in the shape of foretarsi.

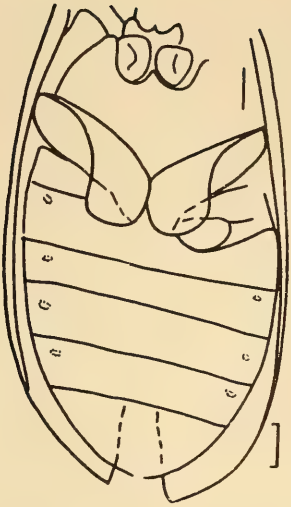

Fig. 7. ? *Necronectes latus*, sp. nov. Holotype PIN No. 3073/151. Shurab-III. Jurassic.

Exedia plana Ponomarenko, sp. nov.
(Plate II, Photo 1; Figure 8)

Species name coined from 'plana' (Greek)—flat.

Holotype. No. 25554/478*, PIN, almost entire impression of beetle, without antennae, fore- and middle tarsi. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area in Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype. In addition, paired elytra of a larger beetle found at the same site, specimen PIN, No. 2239/1322 (elytral length 50 mm, width 11 mm), very similar in shape. Due to large difference in dimensions, its positive inclusion in this species is problematic.

Description. Length of head nearly half the width, deeply retracted into emargination of anterior pronotal margin. Pronotal length half its width at base, its anterior margin half the width of posterior. Prosternum visible in front of forecoxae, prosternal process projecting anteriorly as a flat keel. Mesosternum shorter than large middle coxae, mesepimera strongly broadening towards shoulders. Metasternum roundly tapering anteriorly, length nearly one-third the width; its anterior margin half the width of posterior. Distance between middle and hind coxae greater than length of hind coxae. Length of metepisterna much greater than its width at anterior margin. Width of hind coxae 1.7 times the length, central raised part twice as long as wide. Abdomen slightly broadening to base of second visible sternite and tapering thereafter. First sternite slightly shorter than subequal second and third; fourth sternite two-thirds the length of third and equal to sixth; fifth sternite shorter than them. Elytra with alternate higher and lower ridges.

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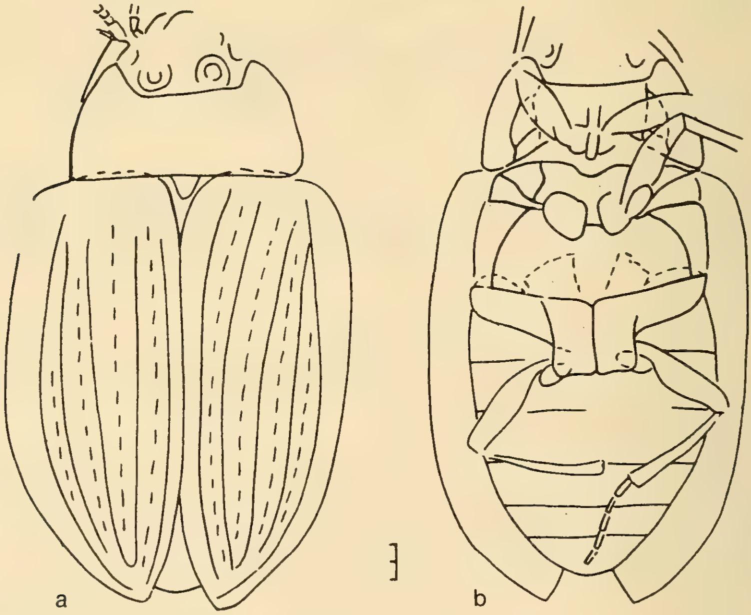
*Given as No. 2554/778 both in Fig. 8 and Plate II, Photo 1—General Editor.

29 Legs rather long. Foretibiae noticeably broadening apically. Middle femora thickening medially, hind femora weakly clavate, broadening in apical third. Hind tibiae equal to femora in length, but much narrower. Hind tarsi much shorter than tibiae. Integument highly sclerotized, with fine punctures.

Dimensions. Body length 32 mm, width 18 mm; elytral length 23 mm.

Genus *Pseudohydrophilus* Deichmüller, 1886

Pseudohydrophilus: Deichmüller, 1886, p. 67; Handlirsch 1906–1908, p. 544; Ponomarenko, 1971, p. 75. *Prodytiscus:* Oppenheim., 1888, p. 237.



29 Fig. 8. *Exedia plana,* sp. nov. Holotype PIN No. 2554/778; a—dorsal view, b—ventral view. Karatau, Upper Jurassic.

Poor preservation of earlier material of this genus precludes exact determination of its taxonomic position. However, definitive chracters do not contradict its inclusion in the Coptoclavidae whereas, all chracters considered together, it cannot be related to any other known taxon. In one specimen, femoral plates chracteristic of Necronectidae may be observed (Ponomarenko, 1971a, Plate VIII, Photo 2). This genus differs from the representatives of the subfamily [Necronectinae] in the structure of the foretarsi, the middle segments of which are not notched apically.

Genus *Stygeonectes* Ponomarenko, gen. nov.

Genus name coined from the mythical River Styx (Greek), and 'nectes' (Greek)—oarsman.

Type species. S. jurassicus sp. nov. Jurassic of Baikal.

Description. Rather large, cylindrical, natatory larvae with long, oar-shaped middle and hind legs. Head sessile, weakly transverse, widest in front of posterior angles, anterior margin nearly linear, nasale absent. Lateral ocelli six, rather large, on a single sclerite* near anterior angles of head capsule. Antennae almost equal to head in length, first and fourth antennal segments much shorter than second and third. Mandibles shorter than their apical width; apical denticles pointed, directed medially. Retinaculum pointed, situated approximately at middle of mandible. Proximal to retinaculum, mandible much wider than distal to it.

Prothoracic tergite longer than meso- and metatergites; first seven abdominal tergites shorter than thoracic and the last abdominal tergite. Femora, tibiae and tarsi of forelegs subequal in length, with short and fine bristles. Middle and hind femora noticeably shorter than tibiae and tarsi. Tibiae and tarsi with dense, long and slender natatory hairs on both sides. Upper margin of tarsi convex. Eighth abdominal tergite transverse; its posterior margin scarcely overhanging the only open spiracles, located below the base of the urogomphi at middle of hind margin. Well-developed tracheae proceed anteriorly from the spiracles. Urogomphi long, rather thick, straight with indistinct segmentation, lacking setae.

Species composition. Monotypic genus.

Remarks. Small, early-stage larvae of *Stygeonectes* closely resemble *Parahygrobia* larvae. They differ in the shape of the mandibles, absence of urogomphal pads and in the fine and dense natatory hairs. However, all these structural features can be noticed in only a very few of the fossil remains. Therefore, the best distinguishing feature is the shape of the middle and hind tarsi. In *Parahygrobia* they are virgate, their upper margin (usually the anterior margin in the impressions) is straight. In *Stygeonectes* the anterior margin of the tarsi is curved, roundly protuberant. *Stygeonectes* displays this unique character while swimming*, *Coptoclava* lavae similarly use the middle and hind pairs of legs for swimming. This similarity forces us to consider *Stygeonectes* and *Coptoclava* as members of one group, whereas *Parahygrobia* remains among the common natatory forms.

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*See our note on page 25—General Editor.

Stygeonectes jurassicus Ponomarenko, sp. nov.
(Plate II, Photos 2, 3; Figure 9)

Species name coined from 'jurassicus' (Latin)—Jurassic.

Holotype. No. 3000/935, PIN, almost entire middle-instar larva. Trans-Baikal, Buryat ASSR, Mukhorshibir region, Novospasskoe settlement (Novospasskoe site). Middle Jurassic, Ichetui series.

Material. Seventy larvae, of which 50 in collection No. 3000 from Novospasskoe site; 4 in collection No. 3053 from Uda site, Buryat ASSR, Eravnin region, Uda river close to Ulan-Mailo (tribal) settlement [village], Udin series; 2 in collection No. 3436 from Borzhe site, Buryat ASSR, Eravnin region, Borzhin depression, well No. 35, depth 154–156 m, Udin series; 4 in collection No. 2363 from Khudoga site, Buryat ASSR, Dzhida region, Dzhida river basin, watershed of Khudoga and Simkhak rivers, Ichetui series; 6 in collection Nos. 1980, 1981, 1982 from Ichetui site, Buryat ASSR, Dzhida region, upper reaches of Ichetui river at Petropavlovka settlement, Ichetui series; 2 in collection No. 2089 from Bukukun site, Chita oblast, Kyrin region, left bank of Bukukun river, Bukukun series; 1 in collection No. 1873 from Ust'-Balei site, Irkutsk oblast, Irkutsk region, Angara river near Ust-Balei settlement, Cheremkhov series; 1 in collection No. 1669 from Iya site, Irkutsk oblast, Tulun region, left bank of river Iya near Vladimirovka village, Cheremkhov series.

Description. Head (Fig. 9, b, d) of late-instar larva almost rectangular, of early-instar noticeably narrowing anteriorly. Head capsule with Y-shaped ecdysial line on vertex ("epicranial suture"), its common stem almost equal in length to the fork. Lateral ocelli ovoid, rather large, distance between them smaller than their diameter. First antennal segment equal in thickness to second segment, but one-fourth its length, third thicker and slightly shorter than second, fourth segment two-thirds as thick as third, scarcely longer than first.

31 Body of larva hardly narrowing posteriorly, flattened dorsoventrally. Its lower part not sclerotized, well-defined sclerites present only at the base of legs. Prothoracic tergite of late-instar larvae approximately one-and-a-half

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*Probably a misprint in the original. Meaning can be restored by replacing "displays" with "uses" or by substituting "for" in place of "while"—Scientific Editor.

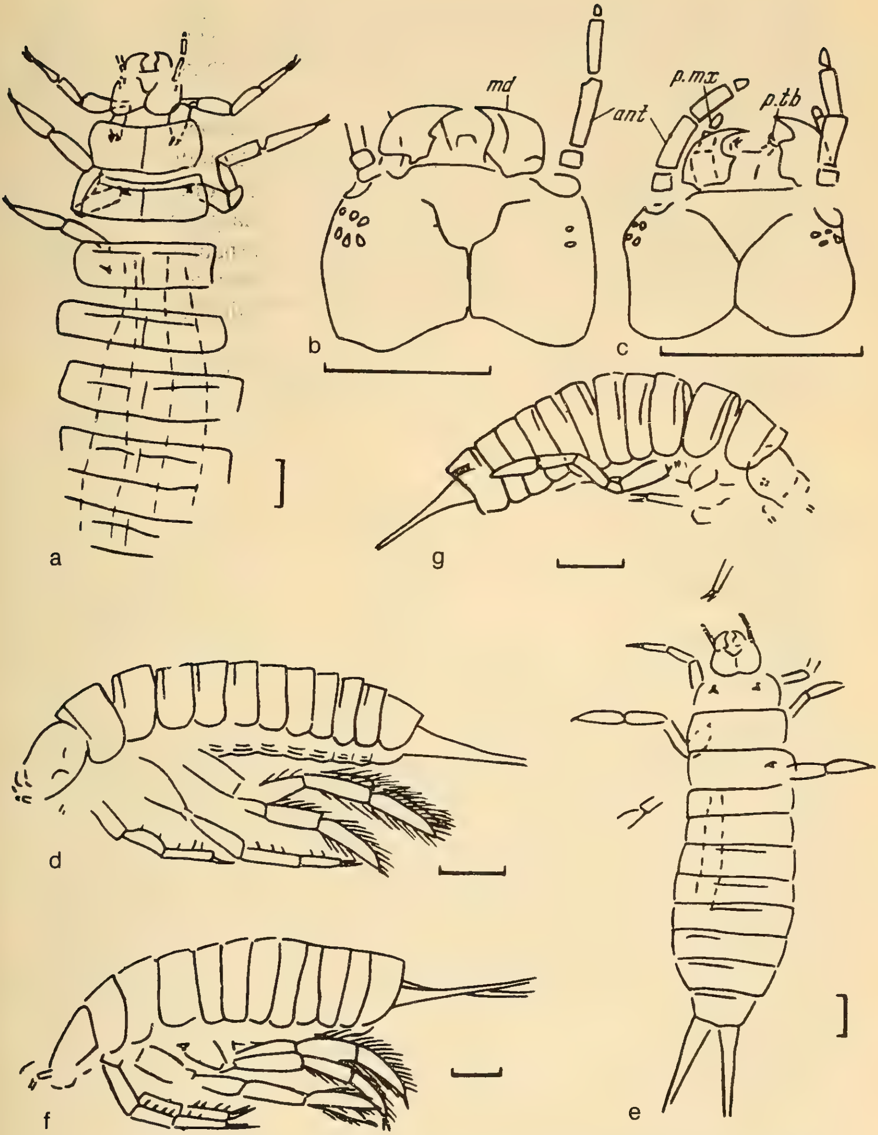

Fig. 9. *Stygeonectes jurassicus*, sp. nov. a, b—holotype PIN No, 3000/935: a—dorsal view, b—head, c—paratype PIN No. 3000/975, head, d —paratype No. 3000/939, e—paratype PIN No. 3000/986; all from Novospasskoe, Jurassic; f—paratype PIN No. 3053/426; Uda, Jurassic; g—paratype PIN No. 1873/11; Ust'-Balei, Jurassic.

times longer than the subequal meso-and metathoracic tergites and almost equal to the eighth abdominal tergite. In early-instar larvae all the thoracic tergites and the last abdominal tergite are subequal, longer than the remaining abdominal tergites.

Forecoxae nearly half the length of forefemora, tibiae and tarsi. Middle and hind coxae longer than forecoxae, slightly shorter than the equal distal segments of legs. Middle tarsi longer than foretarsi, claws of foretarsi much longer than claws of middle and hind tarsi. Posterior margin of middle and hind femora and both margins of tibiae and tarsi with fine natatory hairs, their length exceeding width of the segment. On tarsi, natatory hairs more than ten. Urogomphi more than three times as long as last abdominal segment.

32 *Measurements*

	Larval instars		
	I	II	III
Body without urogomphi	4.8	7–15	21–24
Prothoracic tergite	0.4–0.7	1.0–1.1	1.5–1.8
Mesothoracic tergite	0.3–0.5	0.8–1.0	1.2–1.4
Eighth abdominal tergite	0.4–0.5	1.0–1.2	—
Foretarsi	0.5–0.7	0.8–1.5	2.5
Middle and hind tarsi	0.7–0.8	1.0–1.7	2.3–2.5
Urogomphi	1.5–2.2	2.7–3.2	—

Measurements show considerable variations in the size of *S. jurassicus* larvae, much more than in *Coptoclava longipoda* larvae. Besides the total length varying mainly with the degree of gaseous inflation of the larvae during postmortem putrefaction, the size of the sclerites also varies. However, no regular trends in this variability could be detected. Dimensions vary widely not only in larvae from different sites but also in those from the same Novospasskoe site, where the majority of them were collected. There is wide variation in the size of sclerites of middle-instar larvae. An impression is created that these sclerites are of larvae of two different instars. However, statistical reliability of these differences could not be established on the available material; for now it would be expedient to say that *Stygeonectes* had three larval instars, as is common among beetles.

Ecology. Predatory, actively swimming *Stygeonectes* larvae inhabited small, sparsely vegetated and generally flowing lakes of Western Trans-Baikal and Baikal. The raptorial forelegs and cutting mandibles, very similar to the mandibles of ground beetles of the genus *Carabus*, show that these larvae, like those of *Coptoclava longipoda*, caught their prey with forelegs and then tore it apart. Late-instar larvae are very rarely encountered.

Remarks. Fossil remains of *Stygeonectes* larvae are found in deposits assigned various ages. The Cheremkhov series generally relate to lower Dogger, Ichetui to its upper beds, and the Udin series to lower Malm (Skoblo, 1968). As mentioned earlier, large variability and insufficient material do not permit detection of either reliable differences among larvae collected from various sites or their exact identity.

Subfamily Charonoscaphinae Ponomarenko, Subfam. Nov.

Diagnosis. Large and medium-sized beetles. Hind coxae without femoral plates. Hind tibiae broad and flat; tarsi flat but not broad, much narrower than tibiae. Hind tibiae and tarsi with long natatory hairs.

Composition. Two genera in the Late Jurassic of South Kazakhstan.

Comparison. Differs from the Necronectinae in the absence of femoral plates and expanded hind tibiae, and from the Coptoclavinae in the narrow hind tarsi and natatory hairs.

Genus *Charonoscapha* Ponomarenko, gen. nov.

Genus name coined from Charon of Greek mythology and 'scapha' (Greek)—boat.

Type species. C. grossa, sp. nov. Upper Jurassic of South Kazakhstan.

Description. Large and medium-sized beetles with flattened body. Head small, but transverse. Dorsal eyes well spaced, ventral eyes situated in front of them on both sides of head. Pronotum strongly narrowing anteriorly, in
33 front of deep emargination. Metepisterna not reaching middle coxal cavities. Terminal abdominal sternites shorter than preceding ones. Forecoxae rather long, tibiae slightly longer than femora, first and last segments of foretarsi elongate, but each not longer than three middle segments together. Middle and hind tibiae flat and broad, with a fringe of long and slender natatory hairs. Middle tarsal segments flat and broad in males, but flat and linear in females. Hind tarsi with long, flat and linear segments and natatory hairs. Elytra with protuberant ridges in males, almost smooth in females, with interweaving rows of punctures.

Species composition. Two species in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished by anteriorly deeply emarginate pronotum.

Charonoscapha grossa Ponomarenko, sp. nov.
(Plate II, Photos 4, 5; Figure 10)

Species name coined from 'grossum' (Latin)—large.

Holotype. No. 2554/446, PIN, almost entire impression of male. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides the holotype, one female No. 2997/1847 from the same site.

Description. A large beetle with broad parallel-sided body. Length of head two-thirds its width, deeply retracted into the emarginate anterior

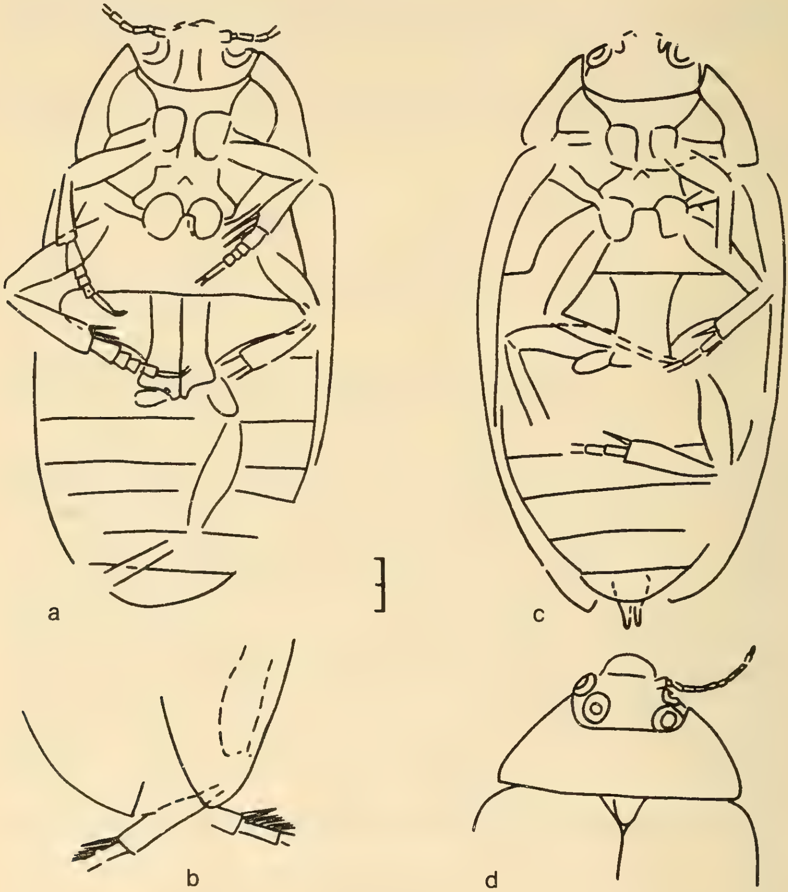

Fig. 10. *Charonoscapha grossa,* sp. nov. a, b—holotype PIN No. 2554/446: a—ventral view; b—dorsal view of posterior end of body; c, d—paratype PIN No. 2997/1847 : c—ventral view; d —head and pronotum. Karatau, Upper Jurassic.

34 margin of pronotum. Antennae slender, filiform, scarcely extending beyond the pronotal base, first segment noticeably larger than the remaining, second short, equal in length and width, remaining segments elongate, last short. Pronotum strongly roundly tapering anteriorly, its anterior margin half the width of posterior, maximum length two-fifths the width. Prosternum anterior to forecoxae shorter than coxae. Propleura wider than long. Prosternal process broadening toward apex. Mesosternum small, shorter than middle coxae, anteriorly with longitudinal groove for the prosternal process. Mesepisterna subequal in length and width. Mesepimera narrow and long, noticeably broadening toward shoulders. Middle small, weakly protuberant, posteriorly covered by metasternal process. Metasternum much shorter than wide, strongly narrowing anteriorly, distance between hind coxae shorter than between middle coxae. Metepisterna short, strongly broadening anteriorly. Hind coxae triangular, short; length about two-thirds the width. Medial raised part of coxa almost three times longer than its width. Abdomen narrowing posteriorly from second visible sternite; last sternite small, short, its length one-third the width. Elytra flattened, epipleura strongly broadening anteriorly. Ridges on elytra rather weak in male, homonomous.

Legs short, foretibiae almost not flattened toward apex, weakly curved; first tarsal segment in male scarcely wider than tibia and one-third its length; second to fourth segments noticeably broadening apically, transverse, very slightly wider than first segment, fifth equal to the first in length, narrow, tapering apically. Tibial spur long, reaching the apex of fourth tarsal segment. Claws short. Middle femora broad, longer than forefemora. Middle tibiae shorter than femur, curved and broadening toward the apex. Middle tarsus a little longer than tibia, its first segment two-fifths the length of tibia, in males its length is twice the width, in females four times the width. Spur of middle tibia not reaching the apex of first tarsal segment. Hind femora approximately equal in size to middle femora, tibiae shorter than them, broadening and flattening toward apex. Tarsi flat, with linear segments. Valvulae sclerotized. Integument with fine, dense punctation.

Dimensions. Body length 24–26 mm, width 12–13 mm; elytral length 18–19 mm.

Comparison. Distinguished by parallel-sided body, strongly anteriorly narrowing pronotum and short last abdominal sternite.

Charonoscapha ovata Ponomarenko, gen. nov.
(Plate II, Photos 6, 7; Figure 11)

Species name coined from 'ovatus' (Latin)—oval.

Holotype. No. 2997/1845, PIN, impression of female without head, abdomen, fore- and middle legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area.

Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, three incomplete remains, one male and two females, specimen Nos. 2066/2393, 2784/1925, 2997/404, from the same site, and one female specimen No. 2452/439 from the Karatau-Galkino site.

Description. Medium-sized beetles with flat, ovoid, posteriorly strongly tapering body. Head together with prothorax forming an almost perfect semicircle. Length of head somewhat less than width, labrum rounded. Antennal segments rather short and thick. Anterior margin of pronotum half the width of posterior, pronotal width 2.3 times the maximum length; anterior margin of pronotum with a deep emargination. Prosternum slightly shorter than forecoxae; prosternal process not broadening posteriorly, propleura slightly longer than wide. Mesosternum short, almost taenioid [ribbon-shaped]. Metepisterna noticeably wider than long; mesepimera strongly broadening toward shoulders. Middle coxae small, slightly projecting; metasternal process between them narrow. Metasternum short, but distance between the middle and hind coxae greater than length of middle coxae. Metepisterna broad, strongly broadening anteriorly. Hind coxae triangular, short, their length nearly half the width; median raised part of coxa twice as long as wide, posteriorly broadening, its outer angle drawn out. Abdomen roundly tapering; beginning with second visible sternite, all sternites of equal length; length of the last sternite two-fifths its width. Elytra of male with distinct, well defined ridges, the four main ridges twice as high as intermediate ones. Elytra of female with numerous dense rows of punctures. Body with fine punctation. Forefemora somewhat dilated, tibiae apically broadening, tarsal segments in female slender, linear. Middle femora longer than forefemora; [the corresponding] tibiae shorter than them, broadening apically, shorter than tarsi. Tarsi linear, with flattened segments. Hind femora shorter than middle femora, slightly broadening in the proximal half. Tibiae slightly curved and flatter in one-third*, noticeably broader than femora and flat; segments of tarsi about half as wide as tibiae.

Dimensions. Body length 15.6–17.9 mm, width 7.5–8.4 mm, elytral length 11.5–12.8 mm.

Comparison. Distinguished by oval, posteriorly narrowing body, and longer last abdominal sternite.

Genus *Charonoscaphidia* Ponomarenko, gen. nov. Genus name coined from genus *Charonoscapha.*

Type species. C. elongata, Upper Jurassic of South Kazakhstan.

Description. Rather large, elongate-oval beetles. Head triangular, almost as long as wide. Dorsal eyes contiguous. Pronotum trapezoidal, narrowing anteriorly, not emarginate anteriorly. Metepisterna not extending to middle coxal cavities. Forecoxae rather long, projecting. Hind tibiae broad and flat, with natatory hairs. Elytra smooth.

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*It is not clear from either the description or the relevant figure which third of the tibiae are so modified—Scientific Editor.

Species composition. Monotypic genus.

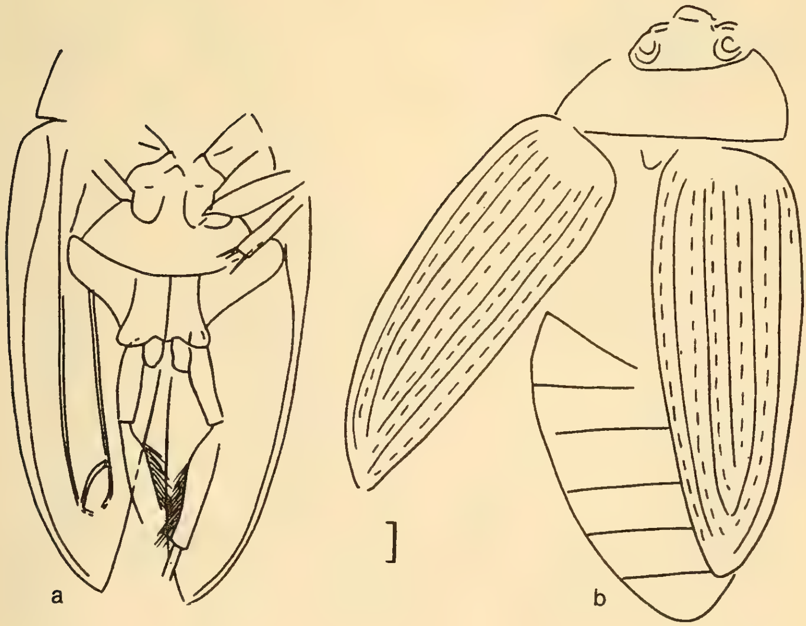
Comparison. Distinguished from genus *Charonoscapha* gen. nov. by a longer head, trapezoidal pronotum without an emargination on the anterior margin.

36 *Charonoscaphidia elongata* Ponomarenko, sp. nov.

(Plate II, Photo 8; Figure 12)

Species name coined from 'elongata' (Latin)—elongated.

Holotype. No. 2384/717, PIN, impression of beetle (female ?) without fore- and middle legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western slope of Kashkarata river valley, Aulie area near Mikhailovka village (Mikhailovka site). Upper Jurassic, Karabastau series.



35 Fig. 11. *Charonoscapha ovata*, sp. nov. a —holotype PIN No. 2992/1845, ventral view; b—paratype PIN No. 2066/2393, dorsal view. Karatau, Upper Jurassic.

Material. Besides holotype, two incomplete impressions of beetles, specimen Nos. 2384/707, 2384/718, and paired incomplete elytra, specimen No. 2066/2591 from the same site. Almost entire impression of beetle, specimen No. 2465/904 from Karatau-Galkino site.

Description. Head triangular, slightly longer than wide, almost not retracted into prothorax. Pronotum not longer than head, anterior margin two-thirds the width of posterior; maximum length half the width of posterior margin. Prosternum shorter than forecoxae; propleura longer than wide. Forecoxae rather long, projecting. Hind coxae triangular, only slightly shorter than wide, their raised middle part three times longer than wide. Abdomen narrowing posteriorly from base, length of the last sternite about half its width. Hind tibiae same length as femora but a little wider than them. Elytra with distinct dense rows of punctures. Body with fine punctation.

Dimensions. Body length 23 mm, width 10 mm; elytral length 16–17 mm.

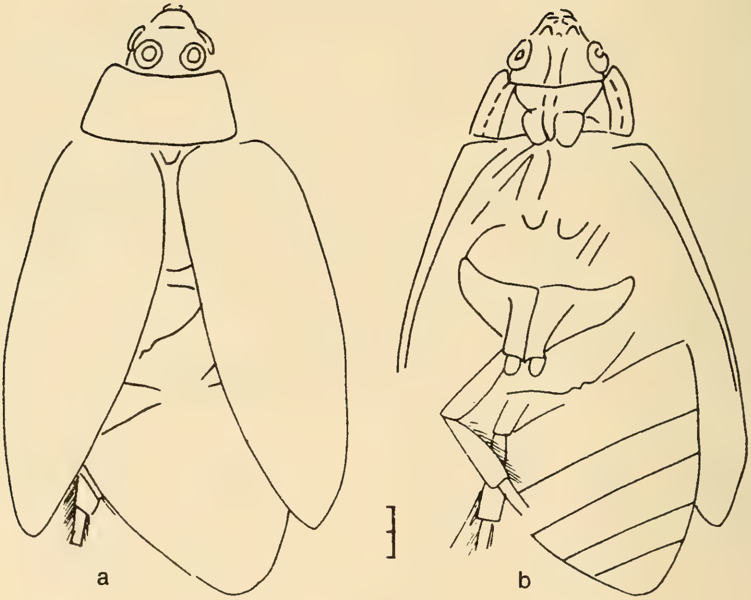


Fig. 12. *Charonoscaphidia elongata* sp. nov., holotype PIN No. 2384/717: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

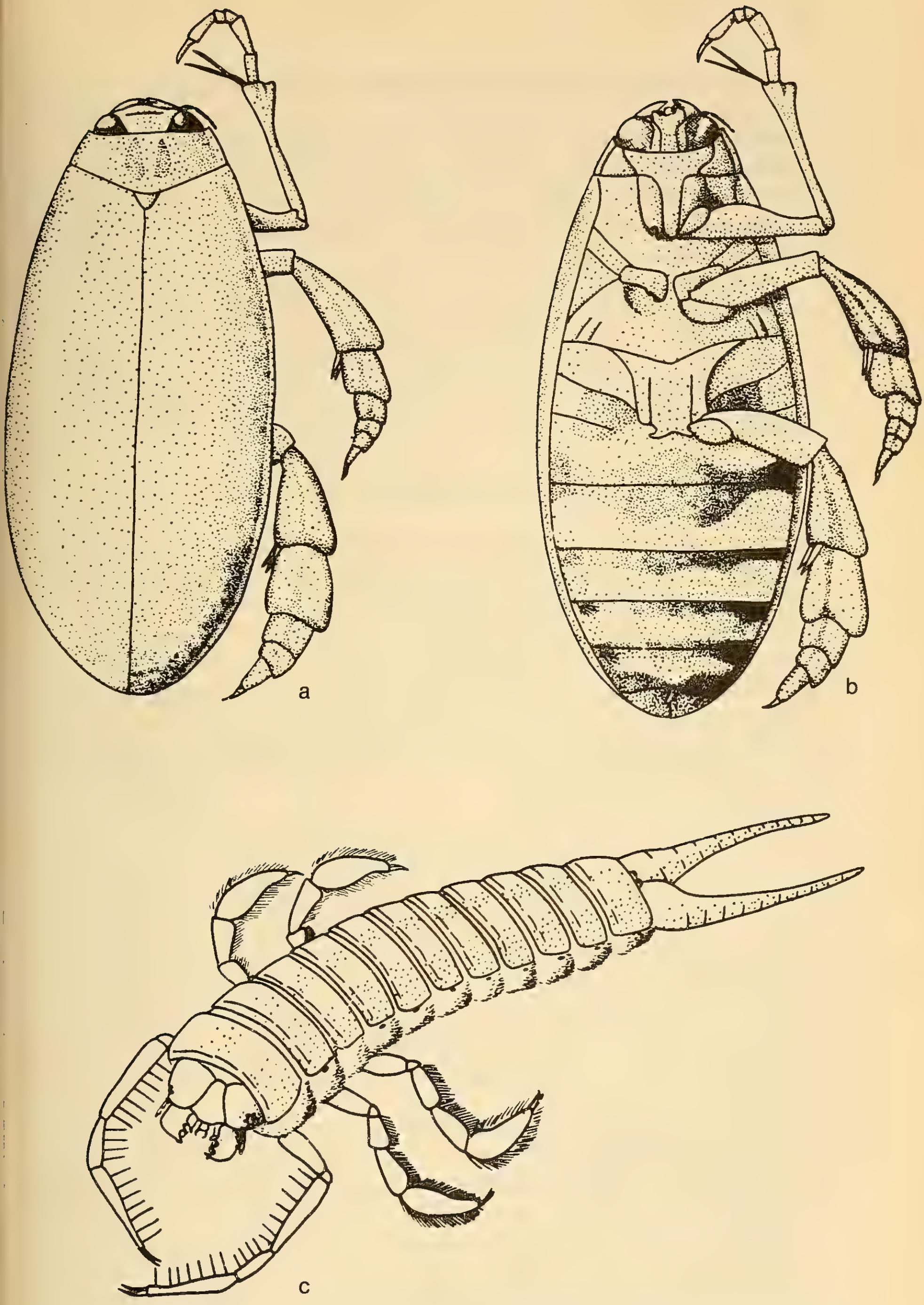


Fig. 13. *Coptoclava longipoda* Ping, reconstructed. a —dorsal view; b—ventral view; c—larva. East Asia, Lower Cretaceous.

Subfamily Coptoclavinae Ponomarenko, 1961

Diagnosis. Large beetles. Hind coxae without femoral plates. Middle and hind tarsi flat and broad, not narrower than tibiae, without natatory hairs. Larvae with mandibles having two denticles on mesal surface, foretarsi much longer than tibiae, middle and hind tarsi broad; urogomphi highly sclerotized, slightly curved.

37 *Composition.* Single genus *Coptoclava* Ping (Fig. 13) in Early (Neocomian) Cretaceous of Trans-Baikal, Mongolia, North and East China.

Comparison. Adult beetles distinguished from members of the remaining subfamilies by homonomous structure of middle and hind legs with distinctly broad tarsi lacking natatory hairs and by mandibles having numerous denticles; larvae are distinguished by the proportions of legs.

Family LIADYTIDAE Ponomarenko, Fam. Nov.

38 *Diagnosis.* Rather small aquatic beetles with oval, biconvex body. Head noticeably retracted into the prothorax, scutellum external. Metepisterna* reaching middle coxal cavities. Metasternum with median longitudinal protuberance, sharply delimited laterally. Hind coxae transverse, not broadening anteriorly, their anterior margin almost straight with small central emargination, bounded in front by an extension of the transverse metasternal suture which forms a single straight line with the anterior margin of the coxae. Legs slender and long. Hind tibiae not shorter than femora and tarsi, very slender, linear. Tarsal segments not broad or oar-shaped. Tibiae and tarsi with natatory hairs.

Composition. One genus in the Mesozoic of Asia.

Comparison. Distinguished from all natatory forms by the very long and slender hind legs, particularly tibiae and tarsi. Differs from Dytiscidae in the presence of a metasternal suture and by the not-anteriorly broadening hind coxae. Differs from Noteridae and Coptoclavidae in the presence of a metasternal suture and metepisterna extending to middle coxal cavities. Differs from Hygrobiidae by the metepisterna extending to middle coxal cavities and by the flat, protuberant area on the metasternum, and from Amphizoidae by the natatory hind legs and flat protuberant area on the metasternum.

Remarks. Liadytidae are plesiomorphic in almost all characters used for distinguishing the families of natatory forms. Only the flat protuberant area on metasternum, uniting Liadytidae and Noteridae, may be considered synapomorphic; but based on the structure of the hind legs, these families occupy extreme positions among the natatory forms—in Liadytidae the legs are longest, and in Noteridae shortest. In the geochronological distribution of Liadytidae, two natatory larvae of highly generalized structure—*Parahygrobia* and *Angaragabus*—were found. The latter even occurred in the same site as one of the species of *Liadytes*. Either of them could be the larva of *Liadytes*, but the difference between them far exceeds the usual interspecific difference between larvae of the same natatory genus [therefore it is highly unlikely that both *Parahygrobia* and *Angaragabus* are synonyms of Liadytes—Scientific Editor].

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*Given as 'Mesepisterna' in the Russian original, but subsequently given as 'metepisterna' in the comparisons with other families—Scientific Editor.

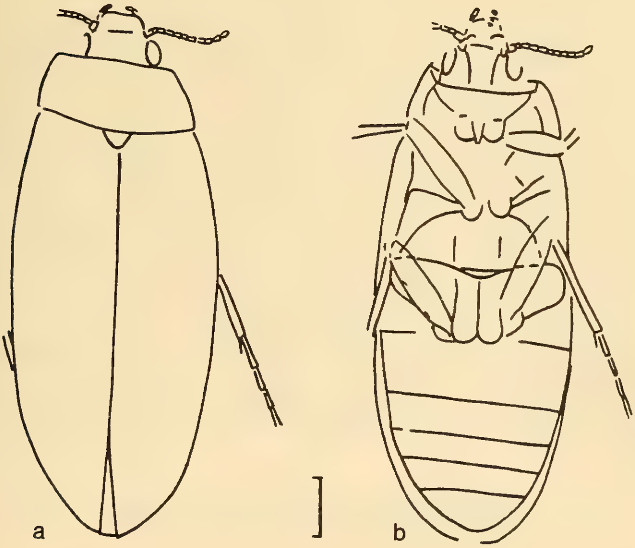
Genus *Liadytes* Ponomarenko, 1963

Liadytes: Ponomarenko, 1963, p. 129.

Liadytes longus Ponomarenko, sp. nov.
(Plate III, Photo 1, Figure 14)

Species name coined from 'longus' (Latin)—long

Holotype. No. 2046/1, PIN, reverse impression of beetle without middle and hind legs. Trans-Baikal, Chitinskaya Oblast, Shelopuginsk region,



39 Fig. 14. *Liadytes longus*, sp. nov.; holotype PIN No. 2046/1: a—dorsal view; b—ventral view. Daya, Lower Cretaceous.

left bank of Daya river, 4.5 km north of Daya settlement (Daya site; Lower Cretaceous, Aptian-Albian, Balei series).

Material. Holotype.

Description. Highly elongate, oval, medium-sized beetles. Length of body exceeds maximum width at posterior third by two-and-a-half times. Head small, two-thirds the width of occiput, tapering straight from base. Genae and temples very short, less than half the diameter of eyes. Antennae weakly moniliform, extending to pronotal base; first segment equal to the following two together; second slightly shorter than third; remaining antennal segments subequal, slightly longer than wide. Gular plate wide, anteriorly broadening, occupying about one-third width of head on posterior margin. Lateral lobes of submentum much larger than median lobe.

Prothorax slightly shorter than head, anteriorly strongly narrowing, anterior margin two-thirds width of posterior. Length of prosternum two-fifths the width at posterior margin. Mesosternum long, not shorter than prosternum. Metasternum transverse, very strongly narrowing anteriorly; 39 anterior margin one-third the width of posterior. Width at posterior margin 2.7 times the length. Posterior extension of metasternum separated by transverse suture, rounded. Metepisterna very strongly broadening anteriorly, their length only slightly more than anterior width. Hind coxae transverse, their lateral length almost half that along midline of body; width 2.7 times the length. Anterior margin of coxa slightly projecting forward from the side. Elevated middle part of coxae posteriorly broadening, rounded at posterior margin; its length two-and-a-half times the width. Length of abdomen nearly half the body length, narrowing posteriorly only from the base of third sternite. First abdominal sternite two-thirds the length of second which is equal to the third and fourth together; fifth very slightly shorter than the fourth; sixth equal to the third, longer than the fourth. Length of sixth sternite two-fifths the width. Middle and hind femora uniformly thickened, three times broader than tibiae. Hind femora, tibiae and tarsi equal in length. Segments of hind tarsi two-thirds the width of tibiae, almost of equal length. Natatory hairs slender, apical spines not visible on segments of hind tarsi. Integument of body with fine, dense punctation.

Dimensions. Body length 9.2 mm, width 3.7 mm; elytral length 7.0 mm.

Comparison. Distinguished by elongate body, slightly antero-laterally broadening hind coxae, and rounded posteromedial extension of metasternum.

Liadytes crassus Ponomarenko, sp. nov.

(Plate III, Photo 2, Figure 15)

Species name coined from “crassus” (Latin)—broad.

Holotype. No. 3015/369, PIN, impression of metathorax, base of abdomen and hind legs. Trans-Baikal, Chitinskaya Oblast, Balei region, right bank of Unda river, 2 km above Zhidka settlement (Unda site). Lower Cretaceous, Aptian-Albian? Balei series.

Material. Holotype.

Description. Oval, medium sized beetle. Length of metasternum one-fourth the width at posterior margin, anterior margin half the width of posterior; posterior margin angularly extending backward in middle third. Longitudinal and transverse metasternal sutures distinct. Hind coxae transverse, only slightly tapering laterally. Their lateral length two-thirds the length along midline of body, maximum length half the width. Anterior coxal margin projecting anteriorly. Elevated middle part of coxa slight tapered posteriorly; posteriorly with lateral notch, apically truncate; length of elevated part more than half its width. Abdomen narrowing posteriorly from third sternite. First abdominal sternite two-fifths the length of second, third half that of second. Hind femur, tibia and tarsus approximately equal in length. Hind femur markedly broadening along almost its entire length, only three times as long as wide. Hind tibia one-fourth the width of hind femur. Three basal segments of hind tarsus equal in length. Spurs of hind tibiae and spines on apices of tarsal segments stiff. Integument of body with rather large distinct punctation.

Dimensions. Body length about 6 mm, width 3.0 mm, elytral length 4.3 mm.

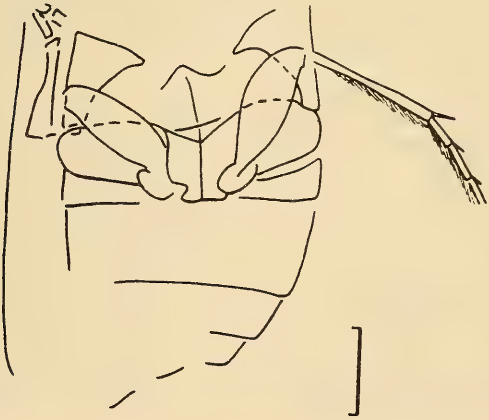


Fig. 15. *Liadytes crassus*, sp. nov.; holotype PIN No. 3015/369. Unda, Lower Cretaceous.

Comparison. Resembles *L. longus*, in the anteriorly extending hind coxae but differs in the posterior triangular extension of metasternum, thicker hind femora, and wider body.

Family DYTISCIDAE Leach, 1815

Genus *Cretodytes* Ponomarenko, gen. nov.

Genus name coined from "creta" (Latin)—chalk, and genus *Dytiscus*.

Type species. C. latipes; Upper Cretaceous, Turon of South Kazakhstan.

Diagnosis. Lateral extensions of metepisterna [metapleurosternites] narrow, triangular; apical recess on anterior projection of metasternum triangular, deep and rather wide. Elevated middle plates of hind coxae slightly diverging posteriorly, not broadening toward apex, apically rounded. Hind legs broad; tibia two-thirds the length of femur, approximately two-and-a-half times as long as wide. Preapical groove and associated tuft of hairs lacking on hind femur. Width of femur at its articulation with the trochanter not narrower than the trochanter.

Species composition. Monotypic genus.

Taxonomic position. A single fossil of thorax and hind legs has been found, a formal comparison of the genus is therefore not possible. *Cretodytes* must belong either to the subfamily Colymbetinae or to the Dytiscinae based on the following characters: metapleurosternites rather wide; middle plate of coxa distinctly notched before its anterior margin, lateral notch absent and apex [= hind margin] rounded. Within the first [= Colymbetinae], based on the broad metapleurosternites and absence of the characteristic hair tuft of the femoral apices, *Cretodytes* would have to be placed in the tribe Colymbetini; the structure of the anterior metasternal extension is also similar. However, such broad and short tibiae are not found in the Colymbetini, moreover the middle plates of the hind coxae are usually broadening towards
41 the apex and strongly divergent in this tribe. Within the Dytiscinae, *Cretodytes* resembles Dytiscini in possessing the fairly broad metapleurosternites and in the position of the middle plates of the hind coxae, but in the Dytiscini, these plates are almost never rounded apically, and such small beetles are unknown. Thus, by indirect characters [evidence], *Cretodytes* cannot be definitely included in any one present-day natatory tribe since it shares features of the most primitive tribes of both Colymbetinae and Dytiscinae. It is hardly advisable, however, to describe a suprageneric taxon from such an incomplete fossil.

Cretodytes latipes Ponomarenko, sp. nov.
(Plate III, Photo 3, Figure 16)

Holotype. No. 2383/256, PIN, impression of metasternum and incomplete hind legs. South Kazakhstan Kyzyl-Ordin Oblast, Chiilii region, northwestern spurs of Karatau range (Kyzyl-Dzhar site). Upper Cretaceous, Turon, Beleutin series.

Material. Holotype.

Description. Rather small beetles. Metasternum strongly transverse, depression on its anterior extension triangular; length of metasternum one-and-a-half times its width, middle part raised and flattened, with narrow median longitudinal furrow. Metapleurosternites triangular, their length between points of greatest proximity with middle and hind coxae is half the distance from the lateral corners of middle coxae to the lateral corners of metapleurosternites. Medial length of metasternum three times the minimum intercoxal distance. Hind coxae longest somewhat lateral to their middle, and laterally tapered beyond. Raised middle part of coxa negligibly narrowing at about midlength; its width one-fourth the length; apical thirds of coxal plates diverge, forming an acute-angled triangle. Hind femora approximately four times longer than wide, three times longer than trochanters. [Hind] tibia not narrower than femur, with longitudinal rows of marginal spines, two spines closer to anterior margin.

Dimensions. Length of fossil remains 4.5 mm, width 6.0 mm; length of beetle thus slightly more than 10 mm and width about 7 mm.

Remarks. Alongside the fossil lay a leg with a very long femur and tibia (Fig. 16b). By its size it could be the middle leg of the same beetle, but dytiscids with such long middle tibiae are not known.

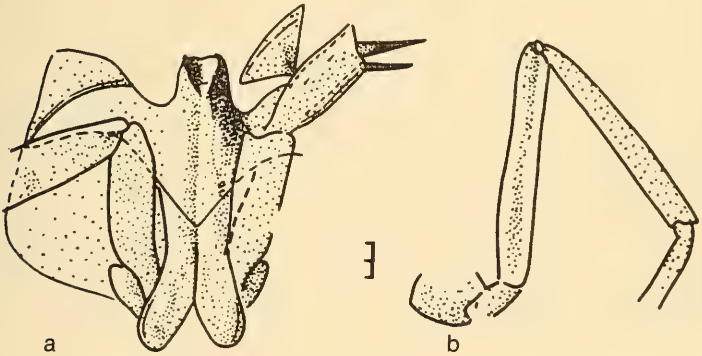


Fig. 16. *Cretodytes latipes*, sp. nov.; holotype PIN No. 2383/256: a—metasternum; b—midleg of probably the same specimen. Kyzyl-Dzhar, Upper Cretaceous.

42 **Family GYRINIDAE Latreille, 1840**

Genus *Avitortor* Ponomarenko, gen. nov.

Genus name coined from 'avus' (Latin)—ancestor, and 'tortere' (Latin)—to whirl.

Type species. A. primitivus, sp. nov. Lower Cretaceous of Trans-Baikal.

Description. Small, flat whirligigs. Head large, highly transverse, approximately equal to prothorax in length. Eyes small, round, ventral eyes antero-lateral to dorsal eyes. Pronotum transverse, anterior margin strongly emarginate. Anterior margin of prosternum straight, prosternal intercoxal process very small. Scutellum exposed, triangular, rather large. Middle coxae oval, almost contiguous, oblique, their length two-thirds the width. Metasternum not shorter than hind coxae. Hind coxae transverse, triangular, their length less than width. Sutures between basal abdominal sternites straight, distinct. Elytra with fine grooves.

Species composition. Monotypic genus.

Comparison. Distinguished from all whirligigs by the long metasternum and narrow middle coxae, and from the present-day forms by the short, transverse hind coxae.

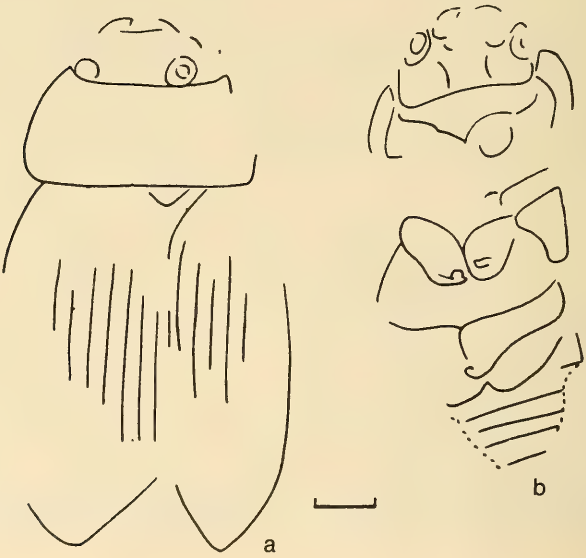


Fig. 17. *Avitortor primitivus*, sp. nov.; holotype PIN No. 3064/856: a—dorsal view; b—ventral view. Baisa, Lower Cretaceous.

Avitortor primitivus Ponomarenko, sp. nov.
(Plate III, Photo 4, Figure 17)

Species name coined from 'primitivus' (Latin)—primitive.

Holotype. No. 3064/856, PIN, impression of beetle without legs. Trans-Baikal, Buryat ASSR, Eravninsk region, left bank of Vitim river below the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanzhin-Goteriv, Zazin series.

Material. Holotype.

Description. Body broadly oval, parallel-sided. Width of head 1.7 times the length, broadest at eyes, slightly narrowing posteriorly from eyes. Dorsal eyes slightly more proximate than vertical*, separated by three times their diameter. Length of pronotum approximately one-third the width, noticeably narrowing anteriorly; anterior emargination of prosternum rectangular, its depth scarcely less than the length of prosternum in front of forecoxae. Middle coxae oblique, irregularly oval, slightly more strongly tapering
43 externally. Length of metasternum two-fifths the width. Distance between middle and hind coxae greater than the length of the latter. Length of hind coxae nearly half their width, lateral margin half the length along median plane. Basal abdominal sternites short, sutures between them distinct, sternites apparently articulate. Elytra with very fine grooves, without traces of punctures.

Dimensions. Body length 10.2 mm, width 5.0 mm, elytral length 6.1 mm.

Genus *Mesodineutes* Ponomarenko, gen. nov.

Genus name coined from Mesozoic and genus *Dineutes*.

Type species. M. amurensis, sp. nov. Upper Cretaceous, Tsagayan of Amur oblast, Arkhara.

Diagnosis. Medium-sized whirligigs, with broad flattened, posteriorly tapering body. Mesosternum transverse, its length half the width, only slightly longer than middle coxae. Middle coxae set apart. Scutellum visible, triangular. Metapleurosternites laterally elongate, their length less than their width or medial length of metasternum. Transverse metasternal suture distinct, almost straight. Hind coxae transverse, their length about half the width. Lateral length of coxa only slightly exceeds its length along longitudinal body axis. Posterior margin of coxa with a deep depression. Abdomen very slightly longer than meso- and metathorax together, uniformly tapering posteriorly from base of third sternite; base of seventh sternite narrower than apex of sixth. First sternite short, suture separating it from second indistinct, second and third longer than fourth to sixth and shorter than seventh. Apex of seventh rounded. Elytra smooth, margined along suture, laterally with wide, anteriorly broadened flange; apex of elytra rounded.

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*So given in the Russian original; obviously a misprint should read "ventral"—General Editor.

Species composition. Monotypic genus.

Comparison. Distinguished from present-day whirligigs possessing smooth elytra by the transverse short hind coxae, from *Angarogyrus* by transverse mesosternum and from *Miodineutes* by short and broad abdomen.

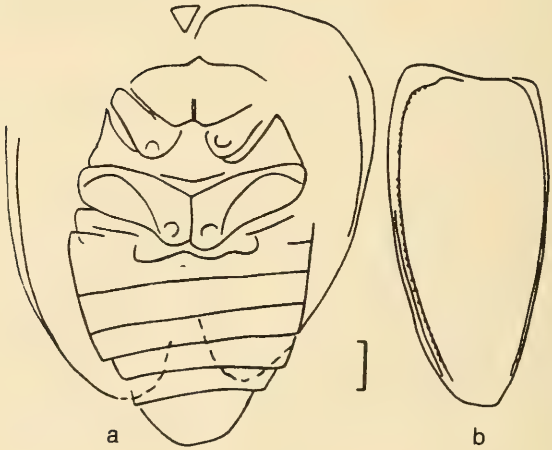
Mesodineutes amurensis Ponomarenko, sp. nov.

(Plate III, Photos 5, 6; Figure 18)

Holotype. No. 2055/74, PIN, beetle without head, prothorax and legs. Amur oblast, quarry at Arkhara station (Arkhara site). Upper Cretaceous, Tsagayan.

Material. Holotype and isolated elytra, specimens No. 2055/79, 2055/100 from the same site.

44 *Description.* Length of beetle exceeds its width by not more than one-and-a-half times, body roundly tapering posteriorly from shoulders. Length of mesosternum two-fifths the width; raised medial part of mesosternum almost triangular; median longitudinal groove proceeding along it posteriorly. Middle coxae slightly tapering laterally, their length about half the width. Intercoxal distance two-fifths the length of middle coxae; distance between



43 Fig. 18. *Mesodineutes amurensis*, sp. nov.; a—holotype PIN No. 2055/74, b—paratype PIN No. 2055/79. Arkhara, Upper Cretaceous.

lateral corners of coxae two-thirds the distance between apex of middle coxa and lateral corner of hind coxa. Hind coxae laterally only very slightly shorter than along median line of body. Width of elevated part of coxa a little less than its length, coxa strongly tapering to lateral third and broadening toward lateral margin. Second abdominal sternite equal in length to third, fourth to sixth equal in length, seventh longer than fifth and sixth together. Apex of seventh sternite with fringe of short stiff hairs. Margins of elytral disk with scarcely noticeable rows of punctures. Elytral surface with very small dense punctation, almost smooth; body ventrally with sparse rather large punctures.

Dimensions. Body length about 11 mm, width 8.5 mm; elytral length 8.0–8.2 mm.

Genus *Angarogyrus* Ponomarenko, gen. nov.

Genus name coined from Angara*, and 'gyros' (Greek)—spinning.

Type species. A. minimus, sp. nov. Middle Jurassic of Cis-Baikal.

Description. Small whirligigs with elongate-oval body. Head large, strongly transverse, longer than pronotum. Eyes round, dorsal eyes behind ventral ones and somewhat more closely grouped. Mesosternum long, almost square, much longer than metasternum. Metasternum short, metapleurosternites forming laterally elongate triangles. Distance between middle and hind coxae half the length of metasternum. Hind coxae markedly oblique, their length half the width, their length at lateral margin half that at the median line of body. Abdomen rather long, uniformly roundly tapering directly from base. Elytra smooth, apically rounded.

Species composition. Monotypic genus.

Comparison. Distinguished from present-day whirligigs possessing smooth elytra by short hind coxae, from the genus *Mesodineutes* by the long mesosternum and less proximate middle and hind coxae, from the genus *Miodineutes* by the broader abdominal apex, and by apically non-truncated elytra.

Angarogyrus minimus Ponomarenko, sp. nov.
(Plate III, Photo 7, Figure 19)

Species name coined from 'minimus' (Latin)—small.

Holotype. No. 1874/30, PIN, impression of beetle without legs. Cis-Baikal, Irkutsk oblast, Tulun region, left bank of Iya river near Vladimirovka (Iya site). Middle Jurassic, Cheremkhov series.

Material. Holotype.

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*Given as Angarida in the Russian original, possibly referring to the Angara River Basin—General Editor.

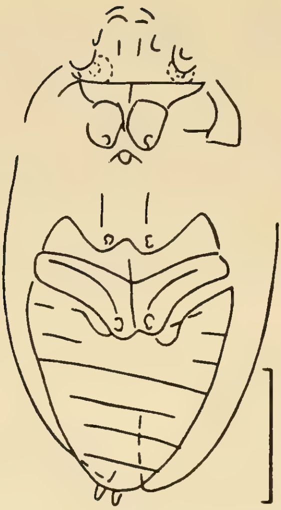

Fig. 19. *Angarogyrus minimus*, sp. nov.; holotype PIN No. 1874/30. Iya, Jurassic.

Description. Body widest in front of middle, tapering posteriorly somewhat more strongly than anteriorly. Dorsal and ventral eyes approximately the same size, considerably overlapping*. Distance between dorsal eyes three times their diameter; distance between ventral eyes and posterior margin of head, half their diameter. Pronotum strongly roundly tapering anteriorly, its length less than one-third the width at posterior margin. Prosternum less than half the length of forecoxae, anterior margin of prosternum straight. Length of propleura markedly less than their width. Forecoxae large, their length not less than length of hind coxae. Mesosternum with a depression on anterior corner and two longitudinal lines in front of middle coxae. Length of metasternum one-fifth its width. Distance between middle and hind coxae half the length of the former. Distance between lateral corners of coxae nearly two-thirds the distance between apex of middle coxa and lateral corner of hind coxa. Abdomen same length as meso- and metathorax together, almost all its sternites equal in length, only the last slightly longer.

Dimensions. Body length 3.7 mm, width 2.2 mm, elytral length 2.8 mm.

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*Probably the eyes are not literally 'overlapping', rather the outlines of the dorsal and ventral eyes are superimposed as in Figure 19—Scientific Editor.

Genus *Cretotortor* Ponomarenko, 1973

Cretotortor archarensis Ponomarenko, sp. nov.
(Plate III, Photo 8, Figure 20)

Species name coined from Arkhara site.

Holotype. No. 2055/75. PIN, impression of left elytron. Amur oblast, quarry at Arkhara station (Arkhara site). Upper Cretaceous, Tsagayan.

Material. Holotype and paired elytra of specimen No. 2055/19 from the same site.

Description. Length of elytron approximately twice the width. Lateral border wider than intervals between elytral grooves, sutural angle obtuse, section of lateral corner only a little longer than that of apical. Elytral interval with transverse rugae and distinct punctures. Suture margined.

Dimensions. Elytral length 6.5–7.1 mm, width 3.2 mm.

Comparison. Distinguished from the second* species of the genus by the wider lateral margin of elytra, the almost equal sections of its apical corners and by the distinct punctures on the elytral intervals.

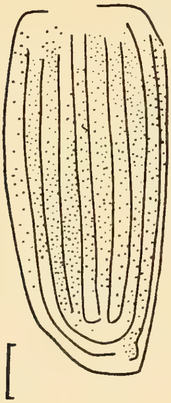

Fig. 20. *Cretotortor archarensis*, sp. nov.; holotype PIN No. 2055/75. Arkhara, Upper Cretaceous.

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*Not described in this treatment—General Editor.

INFRAORDER GEADEPHAGA

SUPERFAMILY CARABOIDEA LATREILLE, 1825

Family TRACHYPACHEIDAE Leconte, 1861

Subfamily Eodromeinae Ponomarenko, Subfam. Nov.

Diagnosis. Clypeus not extending to point of antennal attachment. Forecoxal cavities open. Lateral wall of middle coxal cavities formed by mesosternum, mesepimeron and metasternum. Mesepisternum not extending to middle coxal cavities, minimum separation equal to mesepisternal mesal margin. Hind coxae separating metasternum and abdomen, usually with large femoral plates. Both spurs of foretibiae apical.

Composition. Seven genera in the Triassic, Jurassic and Early Cretaceous of Asia, and possibly the Late Jurassic of Western Europe.

Comparison. Distinguished from the nominal subfamily by the metepisternum extending to middle coxal cavities, while the mesepisternum are farther removed from them.

Genus *Sogdodromeus* Ponomarenko, gen. nov.

Genus name coined from the region Sogdiana and 'dromeus' (Greek)—runner.

Type species. S. altus, sp. nov. Triassic of Soviet Central Asia.

Description. Small, flat beetle. Head transverse, length of head capsule approximately half its maximum width at eyes. Gular plate longer than wide. Antennae rather long and thick, weakly moniliform. Pronotum strongly transverse, widest in anterior third, expanded in front of posterior angles. Mesosternum shorter than the transverse middle coxae. Distance between middle and hind coxae equal to length of middle coxae. Transverse metasternal suture slightly convex posteriorly. Hind coxae slightly oblique, their femoral plates large, in medial half only slightly shorter than coxal width, from this point sharply tapered laterally, but extending to lateral coxal corners as a fairly wide band. Coxae concealed under femoral plates. Length of abdomen half that of meso- and metasternum together, its apex pointed; width of the last sternite half the width of abdominal base. Sternites articulate, movable, telescoping.

Species composition. Monotypic genus.

Comparison. Most closely resembles *Platycoxa* in the possession of large femoral plates fully covering the coxae. Differs from it by the transverse middle coxae and shape of laterally sharply tapered femoral plates.

Sogdodromeus altus Ponomarenko, sp. nov.
(Plate IV, Photo 1; Figure 21)

Species name coined from 'altus' (Latin)—ancient.

Holotype. No. 2971/417, PIN, impression of a beetle lacking most parts of legs and antennae. Soviet Central Asia, Kirgiz SSR, Osh oblast, Batken region, Madygen area (Madygen site, south-western part). Triassic, Madygen series.

Material. Holotype.

Description. Head including mandibles much shorter than broad. Mandibles short. Eyes shorter than temples, longer than very short genae. Length of pronotum two-fifths its width, anteriorly roundly emarginate; anterior angles acute, posterior almost right-angled. Prosternum much shorter than pronotum, longer than forecoxae, anteriorly with flat, longitudinal extension and anterior prolongation of the intercoxal process. [Intercoxal] process flat, 47 broad, broadening behind coxae, truncate apically. Mesosternum slightly shorter than middle coxae. Length of metasternum approximately one-fourth its width, its anterior margin half of posterior margin. Metepisterna strongly broadening toward the anterior margin. Length of femoral plates two-thirds the width, their elongate mesal part not shorter than the apical width; apex weakly rounded. Coxae under femoral plates strongly prolonged along midline of body. Abdomen tapering from the base. First, fifth and sixth visible sternites equal in length; second and third slightly longer; last one-and-a-half times longer than the penultimate, its length two-fifths its width almost triangular. Legs short and weak. Middle femora fusiform, thickened, widest at middle. Tibiae slender, linear, scarcely broadening apically. Middle tarsal segments short, apically broadening a little. Body dorsally with small dense punctation, punctures on elytra fused into transverse rugae. Ventrally with larger punctures, punctures on meso- and metasternum markedly larger, abdominal sternites with dense, longitudinal, slightly convoluted striae.

Dimensions. Body length 9.5 mm, width 4.5 mm; elytral length 6.5 mm.

Genus *Platycoxa* Ponomarenko, gen. nov.

Genus name coined from 'platys' (Greek)—flat and 'coxa' (Greek)—thigh.

Type species. P. armata, sp. nov. Lower Jurassic of Soviet Central Asia.

Description. Small, flat beetles. Head transverse, length of head capsule less than half its width. Temples and genae shorter than eyes. Antennae rather long and thick, their segments only slightly longer than wide. Pronotum strongly transverse, anteriorly not much narrowing. Mesosternum not longer than middle coxae, distance between middle and hind coxae much greater than [length of] coxae themselves. Transverse metasternal suture almost straight. Hind coxae slightly oblique, their femoral plates large, transverse.

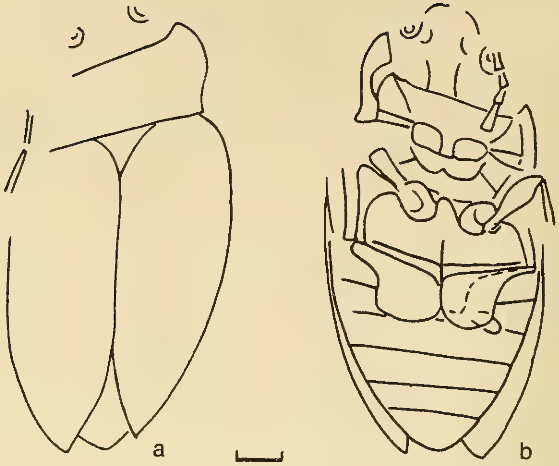

Fig. 21. *Sogdodromeus altus*, sp. nov.; holotype PIN No. 2971/417: a—dorsal view; b—ventral view. Madygen, Triassic.

laterally reduced but extending up to the sides of coxae, here the length of femoral plates not less than that of the coxae, coxae not projecting from under femoral plates. Abdomen rather short, less than twice as long as the meso- and metathorax together, apically pointed, width of the last sternite much less than that of the base of abdomen.

Species composition. Two species in the Early Jurassic of Soviet Central Asia and East Kazakhstan.

Comparison. Distinguished from all other species by shape of large femoral plates of hind coxae, which are laterally not much tapered and extend to the sides of coxae.

48 *Platycoxa armata* Ponomarenko, sp. nov.
(Plate IV, Photo 2; Figure 22a)

Species name coined from 'armata' (Latin)—armed.

Holotype. No. 2903/222, PIN, impression of a beetle lacking antennae and legs. Kirgiz SSR, Ton region, south bank of Issyk-Kul' meander* to the south of Kadzhi-Sai settlement (Issyk-Kul' site). Lower Jurassic, Dzhil' series.

Material. Holotype and impression of metathorax and abdomen of a beetle PIN No. 371/498 from the same site.

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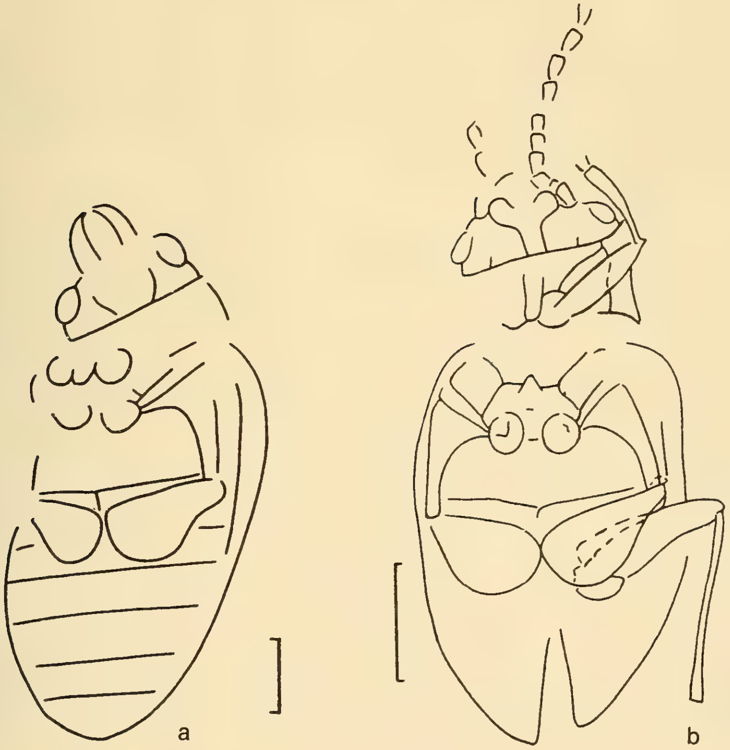
*In the Russian original abbreviated as Iz. for 'izvilina'—General Editor.

Description. Length of head with mandibles greater than length of prothorax, two-thirds the width of occiput. Length of the head capsule two-fifths its width, sharply narrowing anteriorly in front of eyes. Eyes large, almost twice as long as the temples, genae very short. Mandibles long, upright, longer than the head capsule, sharply curved apically. Pronotum almost rectangular, slightly narrower than elytra at shoulders, anteriorly weakly emarginate, its length less than half the width. Posternum in front of forecoxae shorter than coxal length; prosternal process noticeably extending beyond coxae, half the coxal width, apex rounded. Mesosternum shorter than middle coxae. Length of metasternum two-fifths its width at posterior margin, its anterior margin almost one-third the posterior; posterior margin very slightly angularly projecting backward; transverse metasternal suture



49 Fig. 22. Representatives of genus *Platycoxa*. a—*P. armata* sp. nov., holotype PIN No. 2903/222, Issyk-Kul', Lower Jurassic; b—*P. jurassica* sp. nov., holotype PIN No. 2496/6, Kenderlyk, Lower Jurassic.

straight. Distance between middle and hind coxae twice the length of middle coxae. Width of femoral plates of hind coxae 1.7 times the length, tapered in lateral half; their length in lateral third approximately half the maximum length. Abdomen one-and-a-half times longer than meso- and metathorax together, narrowing from the base of fourth sternite; width of last sternite 2.7 times its length, half the width of abdominal base. All abdominal sternites
49 subequal in length. Body with coarse, dense, fused punctation; punctures particularly large on metasternum where they form transverse rugae.

Dimensions. Body length 7.1 mm, width 2.8–3.0 mm; elytral length 5.0–6.0 mm.

Comparison. Distinguished by long crescent-shaped mandibles; long, coarsely punctate metasternum; and less oblique hind coxae.

Platycoxa jurassica Ponomarenko, sp. nov.
(Plate IV, Photo 3; Figure 22b)

Holotype. No. 2496/6, PIN, impression of beetle without apices of antennae, middle legs, fore- and hind tarsi. East-Kazakhstan oblast, Zaisan region, Saur range, right bank of Akkolka river, tributary of Karaungir river (Kenderlyk site), Lower Jurassic, Tologoi series.

Material. Holotype.

Description. Length of head half the width of occiput, sharply narrowing in front of eyes. Genae and temples very short. Gular plate twice as long as wide, much narrower than submentum; lateral lobes of submentum short, round, larger than median lobe. First antennal segment noticeably longer than third which is not longer than fourth; second segment transverse. Pronotum twice as long as wide, anteriorly roundly emarginate, anterior and posterior angles acute, drawn out [away from midline]; lateral margin posteriorly weakly emarginate at middle. Prosternum longer than small forecoxae; prosternal process less than half the width of coxae, distinctly not extending to their posterior margin. Propleura almost triangular, slightly longer than wide. Mesosternum not shorter than middle coxae, in front with triangular depression for prosternal process. Mesepisterna almost rectangular, mesepimera short, taenioid. Length of metasternum one-third its width at posterior margin, its anterior margin half the posterior. Distance between middle and hind coxae one-and-a-half times the length of middle coxae, posterior metasternal margin angularly projecting backward. Metepisterna strongly broadening in anterior third, width of its anterior margin half the length. Length of femoral plates of hind coxae half the width, longest in the mesal third and gradually tapering laterally from there; lateral length of plates one-third their maximum length; posterior coxal margin scarcely peeking from beneath plates at lateral margins. Forefemora noticeably shorter than hind femora, slightly thickened uniformly. Foretibiae slightly shorter than femora, curved, slightly broadened at apex. Hind femora widest in the proximal third, weakly drawn out before apex, three times as long as trochanters. Hind tibiae slender, almost linear, one-fourth longer than femora. Body with small punctures; punctures noticeably larger on metasternum and metepisterna.

Dimensions. Body length 5.0 mm, width 2.5 mm; elytral length 3.7 mm.

Comparison. Distinguished by shorter mandibles, shorter metasternum, and laterally strongly tapering femoral plates.

Genus *Unda* Ponomarenko, gen. nov.

Genus name coined from Unda River.

Type species. U. microplata, sp. nov. Lower Cretaceous of Trans-Baikal.

Description. Small beetles. Head transverse, triangular. Eyes small, not longer than temples. Antennae rather long, slender, filiform. Pronotum transverse, with weak emargination in front, slightly tapering in anterior third. Elytra at shoulders broader than pronotum. Mesosternum nearly equal to middle coxae in length, distance between middle and hind coxae much greater than [length of] middle coxae. Transverse, metasternal suture angularly projecting backward. Hind coxae rather strongly oblique; their femoral plates transverse laterally tapering, extending as narrow tongue up
50 to lateral third of coxa which is posteriorly visible from under them. Abdomen rather short, only slightly longer than meso- and metathorax together, apex pointed; last sternite longer than the remaining, its anterior margin much narrower than base of abdomen.

Species composition. Three species in the Early Cretaceous of Trans-Baikal.

Comparison. Differs in the shape of the femoral plates of hind coxae, which are much shorter than wide, gradually tapering laterally, without notch, and extending up to lateral third of coxae.

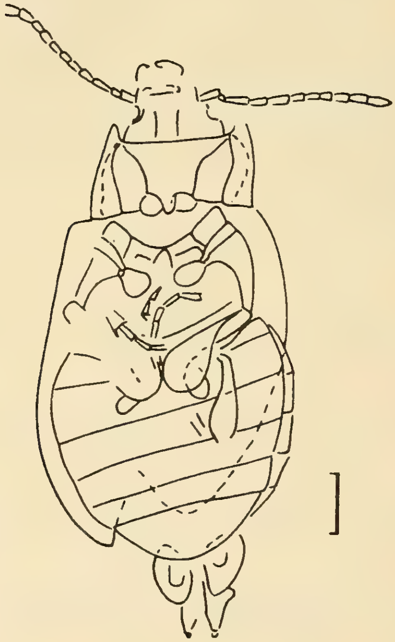
Unda microplata Ponomarenko, sp. nov.
(Plate IV, Photo 4; Figure 23)

Species name coined from 'micros' (Greek)—small; and 'platys' (Greek)—flat.

Holotype. No. 3015/371, PIN, impression of beetle lacking most parts of legs. Trans-Baikal, Chita oblast, Balei region, right bank of Unda river, 2 km upstream of Zhidka settlement (Unda site). Lower Cretaceous, Aptian-Albian?, Balei series.

Material. Holotype.

Description. Head together with mandibles slightly shorter than width of occiput, width of occiput 1.8 times the length of head capsule, the latter narrowing anteriorly from base. Eyes same length as temples, twice as long as genae. Length of gular plate twice its width. Antennae extending beyond the base of pronotum by five segments, segments slightly broadened apically, three apical segments thicker than the rest, distinctly moniliform. First antennal segment equal in length to the third; the second equal to half, and the fourth to two-thirds the third; fourth and fifth longer than sixth to eighth; ninth to eleventh equal in length to the fourth; the last segment teardrop-shaped, pointed apically, its length twice the width. Mandibles short, apically curved. Width of pronotum 1.7 times the length, anteriorly very weakly roundly emarginate. Prosternum 1.5 times longer than forecoxae; prosternal process short, noticeably narrowing posteriorly. Mesosternum with distinct triangular depression for prosternal process, mesepisterna almost rectangular, transverse; mesepimera short, slightly laterally broadened. Length of



51 Fig. 23. *Unda microplata*, sp. nov,; holotype PIN No. 3015/371. Unda, Lower Cretaceous.

metasternum approximately one-third its width at posterior margin, anterior margin narrower than posterior, posterior margin strongly angularly projecting backward, transverse metasternal suture angular. Distance between middle and hind coxae one-and-a-half times greater than [length of] the middle coxae. Mesepisternum strongly broadening in anterior third, its length 1.7 times the width at anterior margin. Hind coxae short, slightly tapering laterally, femoral plates only slightly longer than coxae, not extending to posterior margin of the second abdominal segment, longest in the mesal third, from where it gradually tapers laterally; in the lateral third extending as a very narrow tongue almost up to lateral coxal margins. First abdominal sternite two-thirds the length of second, second longer than third and only slightly shorter than the terminal. Abdomen slightly broadening toward fourth sternite, and then narrowing posteriorly. Base of last sternite two-thirds the base of fourth, twice the length of the last sternite. Sternal lobes of the true eighth segment triangular, valves extended, apically pointed with small stylus. Hind trochanters very broad; hind femora clavate, dilated in
51 apical third; segments of middle and hind tarsi slightly broadening toward apex, not very long. Body with rather dense, small punctures.

Dimensions. Body length 3.8 mm, width 1.9 mm; elytral length 3.0 mm.

Comparison. Distinguished by the long prosternum and shape of femoral plates which are laterally gradually tapered and lacking a distinct postero-lateral angle.

Unda angulata Ponomarenko, sp. nov.
(Plate IV, Photo 5; Figure 24)

Species name coined from 'angulata' (Latin)—angular.

Holotype. No. 2372/24, PIN, impression of almost entire beetle but dismembered into individual sclerites. Chita oblast, Shelopugin region, left bank of Daya river above Shiviya ravine (Daya site). Lower Cretaceous, Aptian-Albian. Balei series.

Material. Holotype.

Description. Length of head slightly shorter than width of occiput, length of gular plate twice its width. Antennae not shorter than head and pronotum together, their segments short, distinctly moniliform, last segment oval, apically rounded. Prosternum in front of forecoxae only a little longer than them; propleura rather wide. Mesosternum shorter than middle coxae, mesepisternum almost triangular, mesepimeron markedly broadening at lateral margin. Length of metasternum two-fifths its width at posterior margin; posterior margin strongly angularly projecting backward, transverse metasternal suture less strongly projecting. Distance between middle and hind coxae almost twice the length of middle coxae. Metepisterna gradually broadening in front of middle, their width at anterior margin two-fifths the

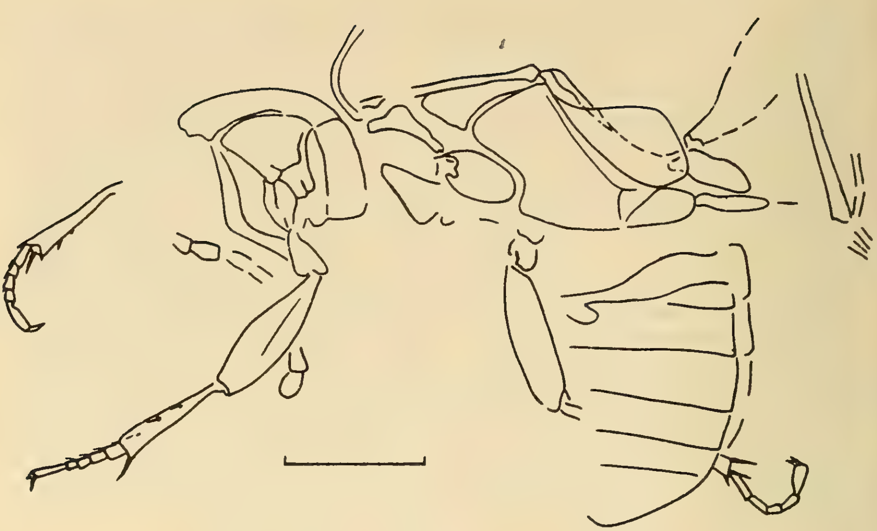


Fig. 24. *Unda angulata*, sp. nov.; holotype PIN No. 2372/24. Daya, Lower Cretaceous.

length. Hind coxae short, slightly tapering laterally. Femoral plates not longer than coxae, their length two-thirds the width, posterior margin in mesal two-thirds truncate at right-angle to body axis; more laterally the femoral plates sharply tapered, extending up to the lateral fourth; postero-lateral angle distinct, almost straight. Abdomen approximately equal in length to meso- and metathorax together, widest at the fourth sternite; basal width of the last sternite half of abdominal base, almost three times wider than long. Foretrochanters equal in length to coxae, one-third the length of forefemora. Forefemora rather thick, widest in apical third, distally narrowing. Tibia a little shorter than femur, somewhat broadening apically; apex of 52 tibia broad and notched, forming an organ for cleaning antennae. Spurs of foretibiae a little longer than first tarsal segment. Tibiae with a row of rather long, stiff spines. Tarsus two-thirds the length of tibia, its first segment thicker and longer than the second, second a little longer than the third and fourth, the last equal to the two preceding together. Middle and hind femora equal in length to forefemora, uniformly broadened, width four times the length. Tibiae slender, linear, one-fourth longer than femora; spurs of middle tibiae slender and short, shorter than first tarsal segment. Middle tarsi two-thirds the length of tibiae, hind tarsi almost equal to them. Tarsal segments, slender, linear. First segment of middle tarsi equal to the second and third together, second longer than third, fourth equal to second, fifth slightly shorter than first. Elytra smooth, body without distinct punctation.

Dimensions. Body length about 6.0 mm, width 2.5 mm; elytral length 4.5 mm.

Comparison. Distinguished by femoral plates with a distinct angle at the posterior margin.

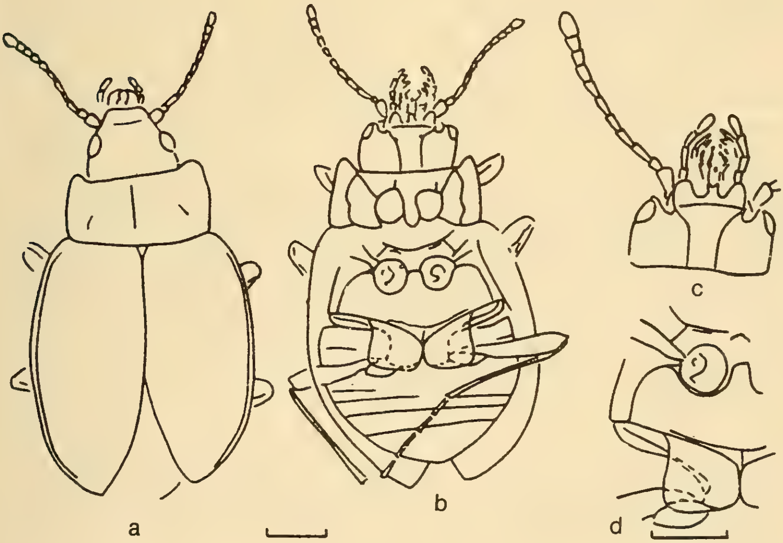
Unda cursoria Ponomarenko, sp. nov.
(Plate IV, Photo 6; Figure 25)

Species name coined from 'cursor' (Latin)—runner.

Holotype. No. 2372/23 PIN, impression of an entire beetle, distal segments of fore- and middle legs bent under body and not visible. Trans-Baikal, Chita oblast, Shelopugin region, left bank of Daya river above Shiviya ravine (Daya site). Lower Cretaceous, Aptian-Albian, Balei series.

Material. Holotype.

Description. Head including mandibles shorter than wide, head capsule almost rectangular, narrowing only in front of eyes, temples a little longer than eyes, genae very short, antennae inserted at anterior margin of eyes. Gular plate longer than wide, anteriorly broadening. Only apical antennal segment extending beyond pronotal base. First segment dilated, twice as long and one-and-a-half times as thick as doliform second; third and fourth equal



53 Fig. 25. *Unda cursoria*, sp. nov.; holotype PIN No. 2372/23; a—dorsal view; b—ventral view; c—head; d—metasternum. Daya, Lower Cretaceous.

to each other and three-fourth the length of first; fifth slightly shorter; sixth to eighth markedly shorter than remaining, almost equal in length and width, last ovoid. Labrum weakly notched apically. Mandibles small, upright, retinaculum weak. Submentum strongly broadening anteriorly; lobes of mentum small, rather narrow, lateral ones larger than middle. Maxillary palps much longer than mandibles. Pronotum almost rectangular, slightly broadening toward anterior third and then slightly narrowing beyond, anterior margin very weakly roundly emarginate, anterior angles rounded, posterior margin slightly projecting backward. Disk of pronotum raised, with median longitudinal groove. Prosternum very short, almost half the forecoxae; prosternal process narrow, extending a little beyond forecoxae, apically rounded. Propleura narrow, twice as long as wide, lateral margin with emargination behind middle; beyond coxae propleuron forming mesally directed short process. Mesosternum short, transverse, half the length of middle coxae, without distinct depression for prosternal process. Mesepisterna almost equal in length and width, rectangular; mesepimera narrow, laterally almost not broadening, taenioid. Middle coxae convergent. Length of metasternum one-third its width at the posterior margin, its anterior margin half of the posterior; distance between middle and hind coxae a little greater than length of middle coxae. Metepisternum strongly and rather sharply broadening in anterior part, its width at anterior margin two-and-a-half times the medial width. Hind coxae strongly reduced in length beyond mesal fourth. Femoral plates not longer than hind coxae, very slightly less in length than width, laterally extending slightly beyond coxal middle, their lateral margins forming an almost straight line parallel to body axis; antero-lateral process absent, postero-lateral angle rounded. Abdomen a little longer than meso- and metathorax together, broadening from base to apex of second visible sternite, 53 then narrowing; third to fifth sternites narrow; width of the last 3.5 times its length, its base two-thirds the abdominal base. Elytra smooth, lateral border narrow. Legs long, femoral apices rather strongly extending beyond lateral body margins. Femora very slightly thickened, forefemora shorter than subequal middle and hind femora. Hind tibiae almost one-fifth longer than femora slender, almost not broadening apically. Hind tarsi four-fifths the tibiae, their first and last segments longer than middle segments, slender, linear. Body smooth, punctation indistinct.

Dimensions. Body length 7.0 mm, width 3.5 mm; elytral length 4.5 mm.

Comparison. Close to *U. angulata* in many characters, but distinguished by the short prosternum, anteriorly strongly broadening metepisterna and narrower femoral plates of hind coxae with rounded postero-lateral angles.

Genus *Psacodromeus* Ponomarenko, gen. nov.

Genus name coined from ‘psakas’ (Greek)—drop, and ‘dromeus’ (Greek)—runner.

Type species. P. gutta, sp. nov. Upper Jurassic of South Kazakhstan.

Description. Medium- and small-sized beetles with teardrop-shaped body. Head including mandibles approximately equal in length and width, triangular, narrowing anteriorly from base. Temples almost as long as eyes, genae much shorter. Gular plate much longer than wide. Antennae long and thick, extending far beyond pronotal base. Pronotum strongly roundly tapering anteriorly from base, at base scarcely narrower than elytra at shoulders. Mesosternum not longer than middle coxae, distance between middle and hind coxae only a little more than the length of middle coxae. Hind coxae with large femoral plates, length of which not less than width; posterior margin of plates straight or rounded and without emargination, lateral emargination shallow. Abdomen less than twice the length of meso- and metathorax together, pointed apically; width of last sternite much less than width of abdominal base. Elytra smooth.

Species composition. Four species in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished from other genera possessing long femoral plates of the hind coxae by the streamlined teardrop-shaped body; laterally, from elytra to head, the body practically describes a single smooth curve.

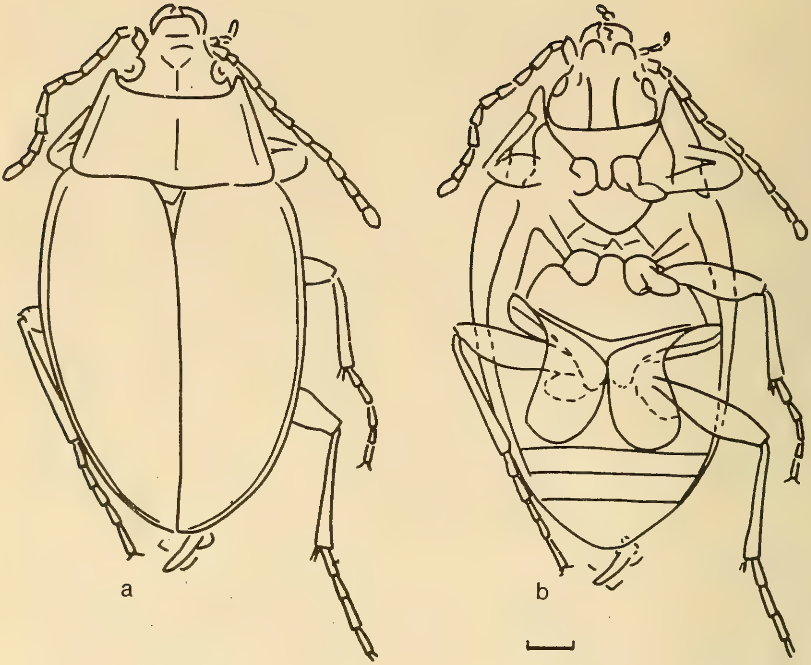
54 *Psacodromeus gutta* Ponomarenko, sp. nov.
(Plate IV, Photo 7; Figure 26)

Species name coined from ‘gutta’ (Latin)—drop.

Holotype. No. 2554/456, PIN, almost entire impression of male. South Kazakhstan, Chimkent oblast, Algabass region south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides the holotype, two almost entire impressions of beetles, specimen Nos. 2066/2514 and 2066/2865 from the same site, and the body of a beetle without head and prothorax, specimen No. 2542/279 from the Karatau-Galkino site.

Description. Head capsule almost half the width of occiput, temples slightly shorter than eyes. Anterior margin of labrum straight. Length of gular plate twice the width. Antennae extending beyond pronotal base by four to five segments. First segment a little thicker than the remaining segments, in length approximately equal to the third, second approximately half that length, fourth noticeably shorter than third, fifth to ninth equal and shorter than fourth, tenth not longer than second, last ovoid. Length of pronotum half



54 Fig. 26. *Psacodromeus gutta*, sp. nov.; holotype PIN No. 2554/456: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

the basal width, anterior margin two-thirds the width of posterior. Anterior margin of pronotum with shallow rounded emargination. Prosternum noticeably shorter than pronotum; prosternal length in front of forecoxae noticeably less than coxal length. Prosternal process apically rounded, its width half that of forecoxae. Mesosternum slightly shorter than middle coxae, with small triangular depression for prosternal process. Mesopleura markedly shifted anteriorly in relation to mesosternum; mesepisterna almost rectangular; mesepimera rather long, slightly broadening laterally. Length of metasternum two-fifths the width at posterior margin, width at posterior margin 1.7 times the anterior. Distance between middle and hind coxae nearly equal to length of the middle coxae. Posterior margin of metasternum slightly angularly projecting backward, transverse metasternal suture almost straight. Metepisterna strongly but not sharply broadening in anterior third. Hind coxae laterally sharply tapering in mesal fourth, nearly untapered

55 beyond; mesal margin almost twice the length of lateral margin. Femoral plates more than twice the length of hind coxae, extending up to mid-abdomen, almost twice as long as medial width; basally drawn out into narrow tongue in the lateral half of coxa and extending to lateral corners of metasternum. Posterior margin of femoral plate rounded, laterally with a shallow emargination. Abdomen 1.7 times longer than meso- and metasternum together, narrowing from the commencement [anterior margin] of fourth sternite; base of last sternite half the width of abdominal base, three times its own length. Legs rather long, femora extending by one-third beyond lateral body margins, gradually broadening toward apical third, distally narrowing, slightly drawn out before apex; forefemora two-thirds the length of middle femora and five-eighths the hind femora. Tibiae very slightly broadening in distal third, foretibiae equal in length to femora, middle and hind tibiae slightly shorter than the corresponding femora, apical spurs of foretibiae small; groove for cleaning antennae oblique. Foretarsi equal in length to tibiae, their basal segments almost equal, apical segment longer than them. Middle tarsi scarcely longer and hind tarsi noticeably longer than the corresponding tibiae; their first segments longer than spurs of tibiae; segments of middle tarsi equal in length; in hind tarsi last segment longer than the remaining [= preceding] segments. Body with small punctures.

Dimensions. Body length 9.8–10.8 mm, width 4.5–5.3 mm; elytral length 6.8–7.7 mm.

Comparison. Distinguished by long femoral plates of hind coxae.

Psacodromeus ovalis Ponomarenko, sp. nov.
(Plate IV, Photo 8; Figure 27)

Species name coined from 'ovalis' (Latin)—oval.

Holotype. No. 2997/1849, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, almost entire impression of beetle, specimen No. 2384/757 from the same site.

Description. Length of head capsule two-thirds the width. Temples scarcely shorter than eyes. Anterior margin of labrum slightly emarginate. Length of gular plate two-and-a-half times the width. Antennae extending beyond pronotal base by four segments. First segment thicker and two-thirds the third, second half the length of third, fifth slightly longer than first, fourth equal to first, remaining except the tenth equal to fifth, tenth slightly shorter, last ovoid. Pronotum anteriorly with rather deep straight emargination, its anterior margin five-sevenths the posterior, length half the basal width. Prosternum slightly shorter than pronotum; length of prosternum in front of

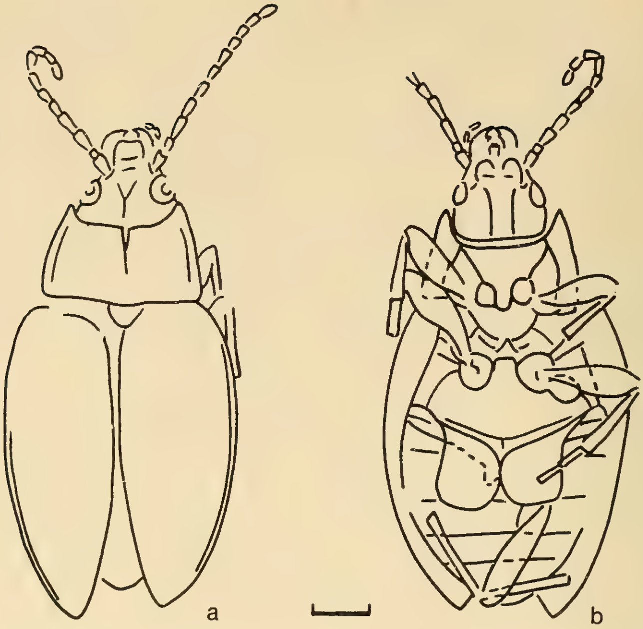


Fig. 27. *Psacodromeus ovalis*, sp. nov.; holotype PIN No. 2997/1849: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

forecoxae very slightly more than coxal length. Prosternal process straight, apically rounded, scarcely longer than hind coxae, two-thirds their width. Mesosternum half the length of middle coxae, triangular depression for prosternal process rather large. Mesopleura somewhat shifted anteriorly in relation to mesosternum, mesepisterna almost rectangular, mesepimera rather long, laterally slightly broadening. Length of metasternum almost one-third its width at posterior margin, width at posterior margin 1.7 times at anterior; distance between middle and hind coxae slightly more than the length of middle coxae. Posterior margin of metasternum very slightly angularly projecting backward; transverse metasternal suture almost straight. Metepisterna sharply broadening in front of anterior margin. Length of hind coxae laterally strongly reduced from mesal fourth, less than half at the lateral than at the mesal margin. Femoral plates 1.7 times longer than coxae, abruptly shortened at midwidth and extending to corners of metasternum as a narrow angular process bordering the anterior coxal margin. Posterior
56 margin of the elongate part of coxa almost straight, postero-lateral angle well defined, shape of postero-lateral part almost rectangular. Abdomen one-and-a-half times longer than meso- and metasternum together, narrowing from

base of second sternite, basal width of the last sternite half of abdominal base, length of last sternite one-fourth its width. Not more than one-fourth of femora extending beyond lateral body margins, femora rather weakly broadening toward middle, distally narrowing; forefemora very slightly shorter than middle femora, four-fifths the length of hind femora. Tibiae very slightly broadening in distal fourth, fore- and middle tibiae two-thirds the corresponding femora, hind tibiae equal to hind femora. Foretarsi not shorter than tibiae. Body with small dense punctures.

Dimensions. Body length 7.2–8.3 mm, width 3.8–4.0 mm; elytral length 5.2–5.7 mm.

Comparison. Distinguished by the shorter and almost rectangular femoral plates.

Psacodromeus crassus Ponomarenko, sp. nov.
(Plate V, Photo 1; Figure 28)

Species name coined from 'crassus' (Latin)—thick.

Holotype. No. 2066/3147, PIN, impression of a beetle without antennae and legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western border of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

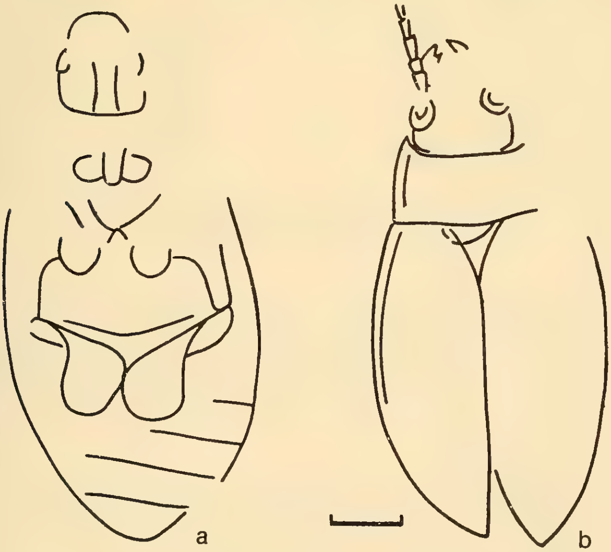


Fig. 28. *Psacodromeus crassus*, sp. nov.; a—holotype PIN No. 2066/3147, b—paratype PIN No. 2066/2349. Karatau, Upper Jurassic.

Material. Besides holotype, impression of beetles lacking legs and a large part of antennae, specimen Nos. 2066/2349, 2904/879, 2997/405 from the same site.

Description. Head including mandibles slightly longer than width of occiput; length of head capsule slmost equal to width; temples not shorter than eyes. First antennal segment slightly thicker and very slightly shorter than third, second half the length of third, third noticeably longer than fourth and fifth. Pronotum anteriorly with rather deep straight emargination, pronotal length half the width; posterior margin 1.3 times the anterior. Length of prosternum in front of forecoxae noticeably more than coxal diameter.
57 Prosternal process extending slightly beyond forecoxae and half their width. Mesosternum half the length of middle coxae, triangular depression for prosternal process rather large. Mesopleura strongly shifted anteriorly in relation to mesosternum. Length of metasternum one-third the width at posterior margin; anterior margin half the width of posterior, distance between [middle and hind] coxae greater than length of middle coxae. Posterior margin of metasternum angularly projecting backward, transverse metasternal suture distinctly angular. Metepisterna sharply broadening in anterior third. Femoral plates of hind coxae strongly shortened in middle. Narrow tongue-like process of anterior margin not extending to lateral corners of metasternum. Length of the elongate part of the femoral plate slightly more than width, its posterior margin rounded. Abdomen slightly longer than meso- and metasternum together; abdominal base 1.7 times the base of last sternite, length of last sternite one-third its width. Body with fine, sparse punctation.

Dimensions. Body length 6.5–7.2 mm, width 2.9–3.4 mm; elytral length 4.2–4.5 mm.

Comparison. Distinguished by long head and rounded femoral plates.

Psacodromeus rugosus Ponomarenko, sp. nov.
(Plate V, Photo 2; Figure 29)

Species name coined from ‘rugosus’ (Latin)—wrinkled.

Holotype. No. 1789/214, PIN, almost entire impression of a beetle. South Kazakhstan, Chimkent oblast, Algabass region, Donner-Bulak area near Uspen settlement (Karatau-Galkino site). Upper Jurassic Karabastau series.

Material. Holotype.

Description. Length of head including mandibles equal to width of occiput; head capsule twice as long as mandibles; temples slightly shorter than small eyes. Length of gular plate twice the medial width. Antennae extending beyond pronotal base by four segments. First antennal segment scarcely thicker than the remaining, length of the first segment together with second equal to third; third one-and-a-half times longer than fourth. Length of pronotum five-ninths the width at posterior margin; anterior margin two-thirds the width of posterior, with deep rounded emargination. Prosternum small, shorter than forecoxae, with flat keel in the middle—the continuation 58 of the prosternal process; propleura large, their length one-and-a-half times the width. Forecoxae rounded, contiguous under the narrow prosternal process. Prosternal process rounded apically, two-fifths the width of coxae, its apex scarcely extending beyond coxae. Mesosternum narrow, mesopleura strongly shifted anteriorly. Length of metasternum one-third the width at posterior margin, anterior margin half the posterior; posterior margin strongly angularly projecting backward; distance between middle and hind coxae almost one-and-a-half times more than the length of middle coxae. Metepisternum in anterior half strongly but not sharply broadening. Hind coxae shortened to about half at mesal fourth, further laterally almost equal in length; anterior coxal margin convex, strongly curved backward toward

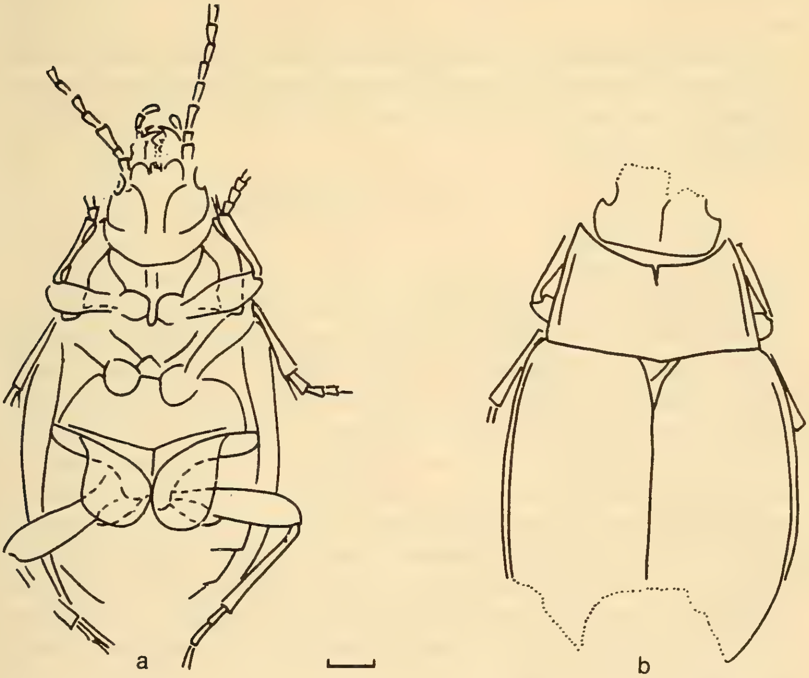


Fig. 29. *Psacodromeus rugosus*, sp. nov.; holotype PIN No. 1789/214: a—ventral view; b—dorsal view. Karatau, Upper Jurassic.

middle of body. Length of femoral plates sharply reduced laterally from the middle of coxae, their narrow tongue-like lateral process basally short, not extending to corners of metasternum. Posterior margin of femoral plates rounded, laterally without emargination. Abdomen only slightly longer than meso- and metasternum together, narrowing from the anterior margin of fourth sternite. Legs rather long, femoral apices noticeably extending beyond lateral body margins. Femora thickened, broadening in distal half, forefemur three-fourths the middle femur, two-thirds the hind femur. Foretibia slightly shorter than femur, noticeably broadening in distal half, notch extending to middle of tibia, spurs of foretibia longer than first tarsal segment. Three basal segments of foretarsus broadened, almost one-and-a-half times longer than wide. Tarsal length apparently almost equal to tibia. Middle tibiae slightly shorter than femur, equal to tarsus; tarsal segments slender, almost equal. Length of hind tibiae equal to femur, slender, slightly broadening from base to apex; tarsus slightly shorter than tibia, its segments slender, linear. Body with rather large punctures, particularly coarse on elytra, pronotum and metasternum.

Dimensions. Body length 10.7 mm, width 5.4 mm; elytral length 6.8 mm.

Comparison. Occupies isolated position among other species of the genus, differs in anteriorly deeply emarginate pronotum, small prosternum with keel, narrow prosternal process, strongly oblique hind coxae, longer legs and distinct punctures.

59 Genus *Karatoma* Ponomarenko, gen. nov.

Genus name coined from Karatau mountain and ‘tome’ (Greek)—cut.

Type species. K. agilis, sp. nov. Upper Jurassic of South Kazakhstan.

Description. Rather large, flat beetles with long legs and mandibles. Length of head including mandibles much longer than width of head capsule; the latter equal to width of head near base, narrowing anterior to eyes; length of temples not less than length of eyes. Antennae long and slender. Pronotum wide, not narrower than elytra at shoulders, very weakly narrowing in anterior third, anteriorly weakly emarginate, anterior angles acute. Metasternum short; distance between middle and hind coxae not longer than middle coxae. Hind coxae with large femoral plates, posterior margin of femoral plates crenate, lateral margin with backward projection straight. Abdomen slightly longer than meso- and metasternum together; basal width of the last sternite two-thirds the abdominal base; apex of abdomen rounded, with small emargination. Elytra with large irregularly distributed punctures. Legs long, hind tibiae longer than femora.

Species composition. One species in the Upper Jurassic of South Kazakhstan and one species in the Lower Cretaceous of Trans-Baikal.

Comparison. Distinguished from other genera with similar shape of femoral plates by the broad, almost rectangular pronotum, long legs, and coarse punctures.

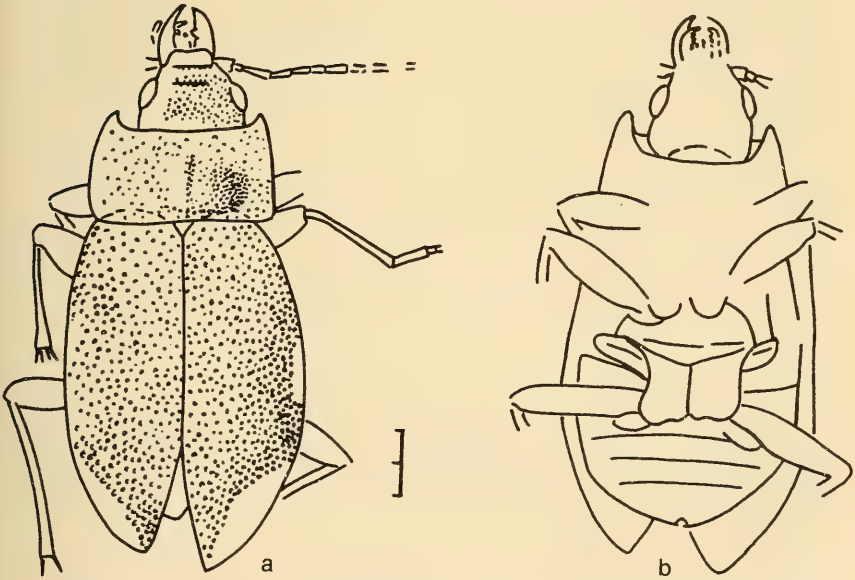
Karatoma agilis Ponomarenko, sp. nov.
(Plate V, Photo 3; Figure 30)

Species name coined from 'agilis' (Latin)—quick.

Holotype. No. 2784/1528, PIN, impression of a beetle without distal segments of forelegs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype. An incomplete impression of a beetle, specimen No. 2997/2442 was found in the same site; of which only the elytra were intact from under which the apices of very long femora and bases of tibiae were visible. Judging from the characteristic features (very coarse punctures, depigmented spots in the apical part of elytra, long legs), the fragment may belong to a beetle of the same species, but its dimensions are almost one-third larger.

Description. Length of head including mandibles one-and-a-half times greater than length of prothorax or width of occiput; temples and eyes equal



60 Fig. 30. *Karatoma agilis*, sp. nov.; holotype PIN No. 2784/1528: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

in length, genae half of them. Antennae extending beyond pronotal base by three segments. First antennal segment a little thicker than flagellar segments, together with second segment equal in length to third; fourth very slightly longer than fifth and noticeably shorter than third. Flagellar segments almost cylindrical, only slightly broadening at apices. Labrum weakly emarginate at apex. Mandibles long, crescent-shaped, asymmetrical, retinaculum small. Width of pronotal base 1.7 times the pronotal length; anterior pronotal angles extending forward; disk of pronotum with raised transverse, oval portion divided by a median longitudinal groove; sides of pronotum not margined. Length of metasternum one-fourth its width at posterior margin, width of posterior margin 1.7 times the anterior; distance between [middle and hind] coxae equal to length of middle coxae, posterior margin of metasternum slightly angularly projecting backward. Transverse metasternal suture almost straight. Femoral plates noticeably longer than coxae, sharply reduced in length at middle; their antero-lateral tongue-like process long, extending up to corners of metasternum. Last abdominal sternite longer than the remaining, two preceding sternites shortest. Femora uniformly thickened almost along the entire length, forefemora slightly shorter than middle femora, middle femora shorter than hind. Middle and hind tibiae very slender, rather sharply broadening only at apex, middle tibiae shorter than corresponding femora, hind tibiae markedly longer. Spurs of middle and hind tibiae shorter than basal tarsal segment. First segment of middle tarsus scarcely broadening toward apex, three times longer than the second. Integument with coarse and dense punctation, elytra with large punctures, medial and apical depigmented spots on lateral margins of elytra without distinct sculpture*, bottom [= underside?] with finer punctation.

Dimensions. Body length 19 mm, width 8 mm; elytral length 12 mm.

Comparison. Distinguished by sharply extended anterior angles of pronotum. Weakly developed raised portion [on disk of pronotum],** long femoral plates, and depigmented spots on the lateral margins of elytra.

Karatoma raptor Ponomarenko, sp. nov.

(Plate V, Photo 4; Figure 31)

Species name coined from ‘raptor’ (Latin)—robber.

Holotype. No. 3015/362, PIN, impression of a beetle without apices of antennae and parts of legs. Trans-Baikal, Chita oblast, Balei region, right bank of Unda river 2 km upstream of Zhidka settlement (Unda site). Lower Cretaceous, Aptian-Albian?, Balei series.

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*Given as structure’ in the Russian original—General Editor.

**Given as ‘weakly expressed relief’ in the Russian original; our interpretation seems reasonable based on the relevant figures and the complete descriptions of the two *Karatoma* spp.—Scientific Editor.

Material. Holotype.

Description. Head including mandibles one-third longer than width of occiput, head capsule slightly shorter than occiput; temples slightly longer than eyes and genae noticeably shorter than them. First antennal segment slightly thicker than flagellar segments, first segment together with second equal in length to the third, second one-third the length of the third; fourth and fifth segments two-thirds the third. Flagellar segments very slightly broadening from base to apex of segment. Mandibles long, slightly incurved, their length almost three times the width; retinaculum small, asymmetric. Width of pronotum 1.7 times its length, anteriorly with trapezoidal emargination, anterior angles almost right-angled, disk of pronotum with transverse raised portion, distant from its posterior margin; with median longitudinal groove anteriorly joining into triangular depression. Sides of pronotum not margined. Mesosternum rather long, only slightly shorter than middle coxae, triangular depression for prosternal process indistinct. Propleura large, almost rectangular, pleural suture oblique, mesepisterna and mesepimera almost equal. Middle coxae transverse, teardrop-shaped, convergent. Length of metasternum two-sevenths the width at posterior margin; width of
61 posterior margin 1.7 times the anterior. Distance between middle and hind coxae equal to length of the middle coxae. Posterior margin of metasternum slightly angularly projecting backward, transverse metasternal suture almost straight. Length of hind coxae strongly reduced laterally, length medially half the maximum length. Femoral plates scarcely longer than hind coxae, almost equal in length and width, occupying somewhat more than half the caxal width, their lateral margin almost straight; antero-lateral process very weakly developed, posterior margin with a slight emargination slightly more mesal to middle, postero-lateral corner rounded. Femora uniformly slightly thickened along the entire length, middle femora slightly broader and shorter than hind femora. Foretibiae very slightly shorter than femora, slightly broadening toward apical fourth, grooves for cleaning antennae short. Middle tibiae scarcely longer than middle femora, weakly curved and broadening from base to apex. Hind tibiae not broader than middle tibiae, noticeably longer than hind femora, broadening only in apical fourth. Lateral margins of middle and hind tibiae with spines; apical spurs shorter than first tarsal segment. Foretarsi equal to corresponding tibiae, middle and hind tarsi noticeably shorter than them. Four basal segments of foretarsi short, somewhat broadening, only slightly longer than wide, last segment narrow, twice as long as the preceding. Middle tarsi three-fourths the length of tibiae, first segment slightly broadened, one-and-a-half times longer than the second, third and fourth equal to second, last segment twice as long as fourth; claws large, straight, scarcely shorter than the fourth segment. Hind tarsi four-fifths the
62 tibiae; first and last segments equal, twice as long as the middle segment; claws large, half the length of middle segment. Integument with coarse

punctation. Punctures on head and prosternum smaller and denser, on metasternum larger and sparser; elytra with large, shallow punctures forming longitudinal rows transversely interconnected, intervals between them forming convoluted transverse rugae. Anterior margin of pronotum with dense longitudinal furrows.

Dimensions. Body length 10.7 mm, width 5.2 mm; elytral length 6.7 mm.

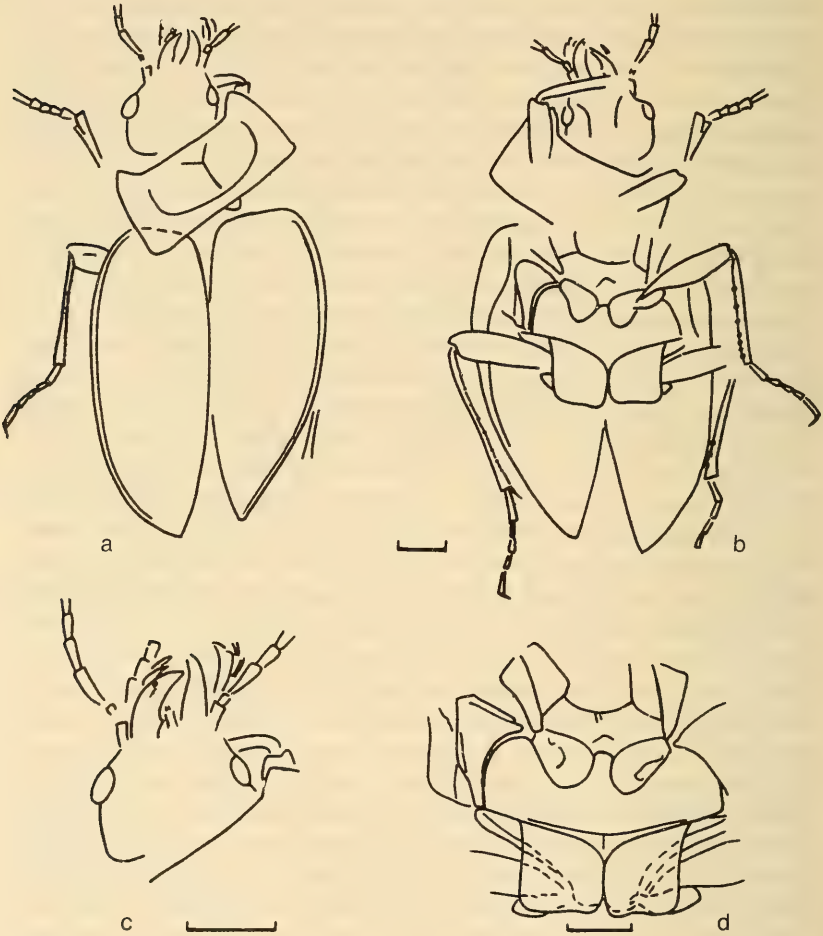

Fig. 31. *Karatoma raptor*, sp. nov.; holotype PIN No. 3015/362: a—dorsal view; b—ventral view; c—head; d—meso- and metathorax, Unda, Jurassic.

Comparison. Distinguished by less acute anterior angles of pronotum, with distinct transverse raised protion on it, and shorter femoral plates of hind coxae.

Genus *Karadromeus* Ponomarenko, gen. nov.

Genus name coined from Karatau mountains and 'dromeus' (Greek)—runner.

Type species. K. rostratus sp. nov. Upper Jurassic of South Kazakhstan.

Description. Small, flat beetles. Head including mandibles a little longer than its basal width, narrowing in front of eyes, length of temples less than length of eyes. Antennae long, rather thick. Pronotum almost rectangular, narrowing only in anterior third, anteriorly very weakly roundly emarginate; its anterior angles acute, extended. Pronotal base much narrower than elytral base. Metasternum rather large, distance between middle and hind coxae greater than the length of middle coxae. Hind coxae with large femoral plates, laterally gradually tapering and extending by narrow tongues almost to the sides of coxae; medial width of femoral plate less than its length. Abdomen a little longer than meso- and metathorax together. Elytra smooth. Legs short, femora scarcely extending beyond lateral margins of body, tibiae shorter than femora.

Species composition. Two species in the Upper Jurassic of South Kazakhstan, and one species each in the Lower Cretaceous of Trans-Baikal and Mongolia.

Comparison. Distinguished from other genera by the anteriorly slightly narrowing pronotum, base of which narrower than elytra, and by the shape of femoral plates of hind coxae.

Karadromeus rostratus Ponomarenko, sp. nov.
(Plate V, Photo 5; Figure 32)

Species name coined from 'rostratus' (Latin)—big-nosed.

Holotype. No. 2904/873, PIN, impression of a beetle without distal parts of antennae and legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Length of head capsule slightly more than two-thirds its basal width; eyes one-third longer than temples; genae long, not shorter than temples. Segments of antennae noticeably broadening from base to apex; first segment thicker than remaining segments, a little shorter than third, together with second longer than third; second one-third of third; fourth noticeably longer than fifth, a little shorter than third; distal antennal segments appro-

ximately equal to fifth. Mandibles short, not projecting anteriorly. Width of pronotum 1.8 times the length, anterior margin very slightly narrower than posterior; posterior margin weakly roundly protuberant. Prosternum slightly shorter than pronotum; length of prosternum in front of forecoxae equal to coxal length. Intercoxal prosternal process half the coxal width, extending beyond coxae and broadening, apex rounded. Length of propleuron twice its width. Length of mesosternum half the midddle coxae, triangular depression for prosternal process small. Mesepisterna almost rectangular, transverse;
63 mesepimera strongly broadening laterally. Length of metasternum half the width at the posterior margin; width at posterior margin 1.7 times at anterior; distance between middle and hind coxae noticeably longer than middle coxae; mesepisterna not sharply broadening in anterior half. Femoral plates of hind coxae laterally rather sharply tapering, their elongate part noticeably longer than their width, narrower than half the coxal width. Reduced part of the femoral plate in the form of a narrow angular tongue extending a little beyond the metasternal corner. Abdomen narrowing from base of fourth sternite, base of last sternite two-thirds of the abdominal base, its width 3.5

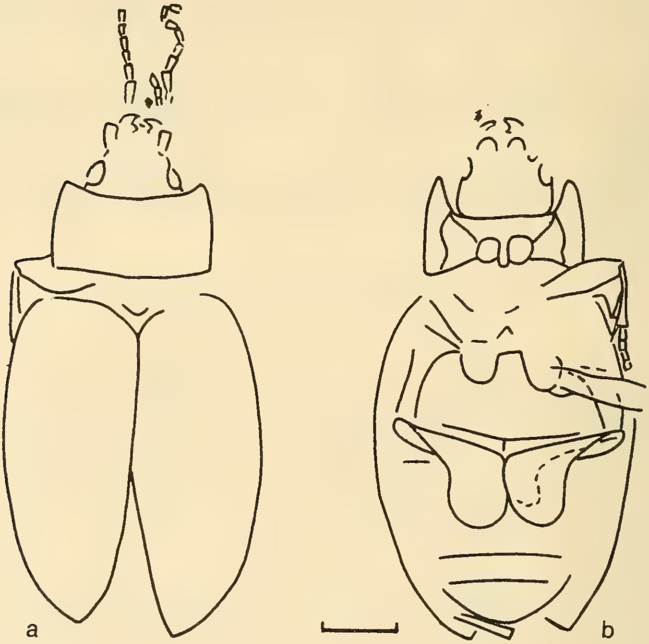

Fig. 32. *Karadromeus rostratus*, sp. nov.; holotype PIN No. 2904/873: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

times the length. Forefemora two-thirds the middle femora; middle femora noticeably shorter than hind femora; forefemora dilated at middle; middle and hind femora uniformly weakly thickened along the entire length. Foretibia almost two-thirds the femur, with deeply incised groove for cleaning antennae. Segments of foretarsi short and broad, only slightly longer than their apical width. Body with small but distinct punctures.

Dimensions. Body length 7.2 mm, width 3.7 mm; elytral length 4.8 mm.

Comparison. Distinguished by the broader and shorter pronotum and the abdomen less narrowed posteriorly.

Karadromeus latus Ponomarenko, sp. nov.
(Plate V, Photo 6; Figure 33)

Species name coined from 'latus' (Latin)—broad.

Holotype. No. 2384/567, PIN, reverse impression of beetle without distal parts of antennae and legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, an inpression of a beetle lying on its side, specimen No. 2554/724 from the same site. Due to lateral disposition of this

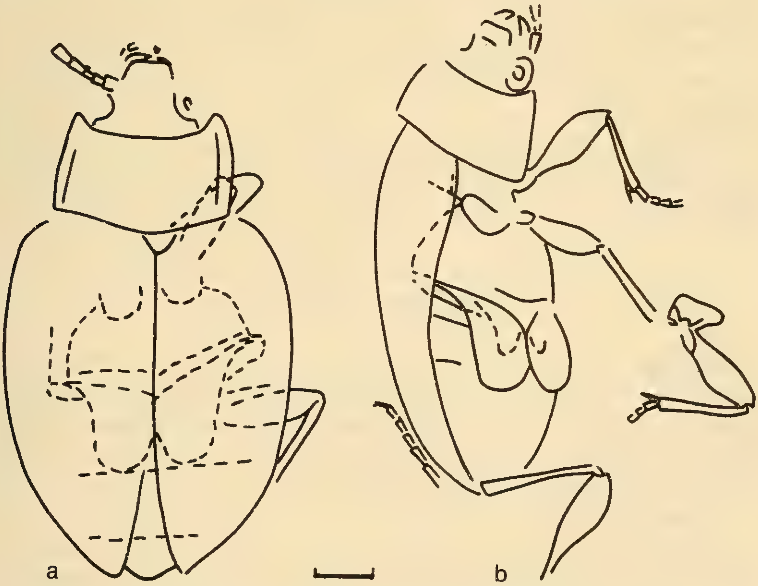

Fig. 33. *Karadromeus latus*, sp. nov.; a—holotype PIN No. 2384/567; b—paratype PIN No. 2554/724. Karatau, Upper Jurassic.

specimen, the shape of pronotum cannot be determined and hence its formal inclusion in this species cannot be considered conclusive.

64 *Description.* Head equal in length and width, narrowing anteriorly from base; temples half the length of eyes; genae short. Antennal segments broadening slightly from base to apex; first segment noticeably thicker than remaining segments; first segment together with the second equal in length to third. Labrum very weakly emarginate at apex. Mandibles rather short, projecting a little from under labrum. Width of pronotum 1.6 times its length; width at its anterior margin nine-tenths that at the posterior; anterior angles blunt; middle of posterior margin angularly projecting backward; pronotum much narrower than elytra at shoulders. Width of metasternum at posterior margin 2.2 times its length, anterior margin narrower than posterior; distance between middle and hind coxae noticeably greater than the length of middle coxae. Metepisterna strongly but not sharply broadening in anterior half. Elongate part of femoral plates one-and-a-half times longer than its width. Abdomen narrowing from base of third sternite, basal width of last sternite half of abdominal base, its length one-fourth its width. All femora are weakly clavate, their widest part at apical third approximately twice that at apex; middle and forefemora* almost equal, slightly shorter than forefemora. Tibiae slender, slightly broadening from base to apex; fore- and middle tibiae slightly shorter than femora, hind tibiae equal to the corresponding femora; apical spurs of tibiae short. Tarsi slightly shorter than tibiae, segments of fore- and middle tarsi short, somewhat broad, segments of hind tarsi almost linear. Body with small dense punctation.

Dimensions. Body length 8.5–9.3 mm, width 5.3 mm; elytral length 5.8–6.2 mm.

Comparison. Distinguished by narrow pronotum which is much narrower than the elytra at shoulders, and the more strongly posteriorly narrowing abdomen.

Karadromeus elongatus Ponomarenko, sp. nov.

(Plate V, Photo 7; Figure 34a)

Species name coined from ‘elongatus’ (Latin)—elongate.

Holotype. No. 3015/363, PIN, impression of a beetle without apices of antennae and of almost all legs. Trans-Baikal, Chita oblast, Balei region, right bank of Unda river, 2 km upstream Zhidka settlement (Unda site). Lower Cretaceous, Aptian-Albian?, Balei series 65

Material. Holotype.

Description. Body of beetle elongate, cylindrical. Head noticeably longer than its basal width; temples and genae slightly shorter than eyes.

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*An obvious misprint in the Russian original. Should read ‘hind’ instead—General Editor.

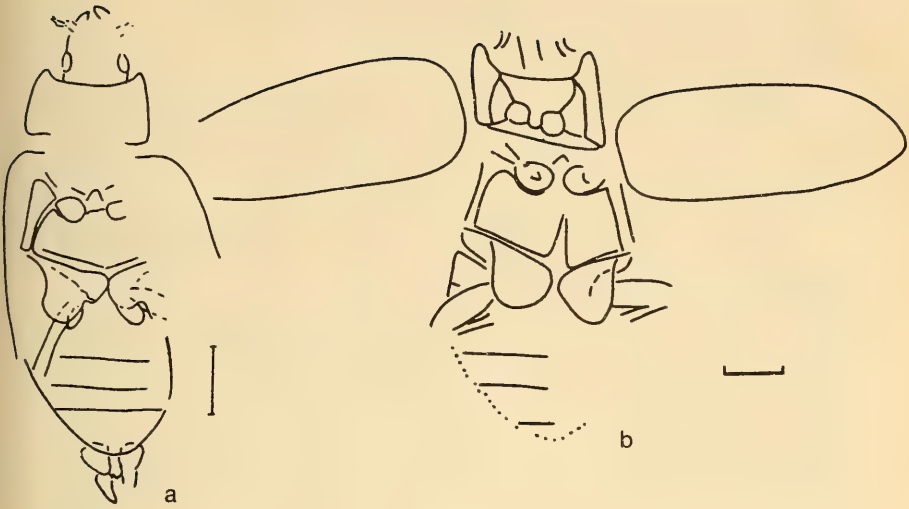

Fig. 34. Species of genus *Karadromeus*. a—*K. elongatus*, sp. nov.; holotype PIN No. 3015/363, Unda, Jurassic; b—*K. mongolicus*, sp. nov.; holotype PIN No. 3145/753. Mongolia, Anda-Khuduk, Lower Cretaceous.

Second antennal segment half the third. Pronotum slightly narrowing in the anterior fourth, its basal width 1.7 times its length; anterior margin weakly roundly emarginate. Mesosternum short, depression for prosternal process large. Mesepimera almost taenioid, very slightly broadening laterally. Metasternal length one-third the width at posterior margin; width at anterior margin half that at the posterior; distance between middle and hind coxae one-and-a-half times longer than middle coxae. Metepisterna weakly and gradually broadening in anterior two-thirds. Hind coxae short, weakly and gradually tapering laterally. Elongate part of femoral plates medial, plates mesally and laterally tapered, with an emargination at the mesal margin, lateral tapered part almost extending up to lateral ends of coxae. Abdomen more than one-and-a-half times longer than meso- and metathorax together, narrowing from base of fourth sternite, sutures between basal sternites not noticeable. Length of last sternite one-third its basal width; its base two-thirds the width of abdominal base. Lobes of eighth true sternite small, imperfectly teardrop-shaped; parameres asymmetrical, short, not perfectly triangular. Hind femora slightly thickened. Body very sparsely punctate.

Dimensions. Body length 4.3 mm, width 1.9 mm; elytral length 2.9 mm.

Comparison. Distinguished from the remaining species by elongate, narrow body, long abdomen, long last abdominal sternite, and shape of femoral plates with a notch at mesal margin.

Karadromeus mongolicus Ponomarenko, sp. nov.
(Plate V, Photo 8; Figure 34b)

Species name coined from Mongolia.

Holotype. No. 3145/753, PIN, impression of a poorly preserved beetle with spread out elytra. Mongolia, Uver-Khangai aimak, Ushugiin-Nuru range, western sources of Shand-god near Anda-Khuduk pit (Anda-Khuduk site). Lower Cretaceous, Neocomian, Anda-Khuduk series.

66 *Material*. Besides holotype, impression of a poorly preserved beetle, No. 3145/754 from the same site. It is possible that some of the isolated elytra collected there also belong to this species.

Description. Length of head capsule noticeably less than its width; eyes slightly longer than temples; genae approximately half the length of temples. Width of pronotum 1.3 times its length, broadest immediately in front of middle from where it roundly tapers anteriorly and posteriorly; anterior margin a little narrower than posterior. Prosternum much shorter than pronotum, in front of forecoxae equal in length to coxae. Prosternal process half as wide as coxae, scarcely extending beyond posterior margin of coxae, apically rounded. Propleura narrow, more than twice as long as wide. Mesosternum half the length of middle coxae; triangular depression for prosternal process large, wide. Mesepisterna small, rectangular; mesepimera long, laterally noticeably broadening. Metasternum approximately two-and-a-half times longer than wide, very slightly narrowing right up to the anterior margin; its anterior margin two-thirds the posterior; distance between coxae greater than one-and-a-half times the length of the transverse middle coxae. Metepisterna very slightly broadening almost up to the anterior margin, [greatly] broadening only along the anterior margin itself; width at anterior margin one-third the metepisternal length. Width of hind coxae sharply reduced beyond mesal third; their maximum length two-and-a-half times the medial length. Femoral plates large, width of their elongate part more than half that of coxae, rather sharply reduced laterally. Abdomen narrowing from beginning of fourth sternite. Hind legs short, femoral apices scarcely extending beyond lateral margins of body, femora slightly thickened, broadest part a little distal to middle. Tibiae noticeably shorter than femora, rather thick, almost not broadening apically. Elytra smooth; traces of two grooves noticeable only in the sutural part. Body with small punctures.

Dimensions. Body length 6.5–7.0 mm, width 2.8–3.0 mm; elytral length 4.7–5.0 mm.

Comparison. Distinguished from other species by the long pronotum and long, very slightly anteriorly narrowing metasternum.

Remarks. The fossils described here are very poorly preserved. Although considerable chitin has been retained in the impressions, it is difficult to study their structure precisely. Hence the interpretation of the observed structures cannot be defended with total certainty. The structure of hind coxae is particularly unclear. At the same time, the structure of the anteriorly very slightly broadening metepisterna makes this form very interesting, exhibiting the characteristic tendency towards closure of middle coxal cavities found in the present-day ground beetles, which is rare in the Mesozoic beetles.

Genus *Eodromeus* Ponomarenko, gen. nov.

Genus name coined from 'eos' (Greek)—early, and 'dromeus' (Greek)—runner.

Type species. E. fasciatus sp. nov.Lower Cretaceous of Trans-Baikal.

Description. Small, flat beetles. Head including mandibles shorter than its length*, triangular, temples and genae shorter than eyes. Antennae short, scarcely extending beyond pronotal base, segments thick, flagellar segments only a little longer than broad. Pronotum almost rectangular, anteriorly very weakly emarginate, anterior angles not sharp, pronotal base slightly narrower than elytral base. Mesosternum with distinct triangular depression for prosternal process. Femoral plates of hind coxae emarginate at posterior and lateral margins. Legs short, hind tibiae not longer than femora.

Species composition. One species in the Upper Jurassic of South Kazakhstan, three species in the Lower Cretaceous of Trans-Baikal.

Comparison. Distinguished from other genera by the shape of femoral plates of hind coxae which are emarginate at posterior margin and strongly so laterally. In addition, differs from most representatives of the family by the almost rectangular pronotum.

67 ### *Eodromeus antiquus* Ponomarenko, sp. nov.
(Plate VI, Photo 1; Figure 35)

Species name coined from 'antiquus' (Latin)—ancient.

Holotype. No. 2239/897, PIN, impression of an almost entire beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site); Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head with mandibles**. Maximum width of head capsule 1.7 times its length, head narrowing anteriorly from base. Eyes slightly longer than temples, genae short. First antennal segment slightly thicker than the

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*Correct as per the Russian original. Should read "width"—General Editor.

**There seems to be an omission in the Russian original. The completed phrase would have drawn a comparison between the length of the head, including the mandibles, and its width. If Figure 35 is drawn to scale, these two dimensions are approximately equivalent—Scientific Editor.

rest, scarcely shorter than third, one-and-a-half times longer than second; second noticeably longer than broad. Flagellar segments commencing from fourth almost equal, only slightly longer than second. Labrum rather deeply emarginate at apex. Mandibles one-and-a-half times longer than wide, apically incurved. Palpal segments short, rather thick. Lateral lobes of mentum large, not shorter than their width. Gular plate narrow, its length almost three times the medial width. Width of pronotum 1.8 times the length, anterior margin almost the same length as posterior, with very slight trapezoidal emargination, posterior margin weakly, roundly protuberant. Pronotum broadest in the anterior third. Prosternum slightly shorter than pronotum, anterior to forecoxae its length equal to that of forecoxae. Width of prosternal process half that of coxae, almost not extending beyond them. Length of propleuron twice the width. Mesosternum rather long, not shorter than middle coxae, triangular depression narrow. Mesepisterna almost rectangular, mesepimera very slightly broadening laterally. Middle coxae converging, a little longer than broad. Metasternal width at posterior margin 3.3 times
68 its length, width at posterior margin 2.2 times that at the anterior. Distance between middle and hind coxae equal to length of middle coxae. Transverse metasternal suture almost straight. Hind coxae from middle almost not tapered laterally, lateral margin half the medial. Length of femoral plates sharply reduced from middle laterally; rather wide, angular lateral process along the anterior coxal margin almost reaching the corners of metasternum. Emargination on posterior margin of femoral plates wide and shallow, lateral emargination deep. Abdomen slightly broadening from base to the third sternite, and tapering beyond; width of last sternite two-thirds the abdominal width*, last sternite one-third as long as wide. Femora gradually dilating, clavate, widest in apical third. Forefemora noticeably shorter than middle femora, and two-thirds the hind femora. Tibiae rather thick, middle and hind tibiae noticeably broadening in apical fourth, hind tibiae weakly broadening from base, not broadening before apex. Fore- and middle tibiae equal in length, hind tibiae 1.7 times longer. Groove on the foretibiae extending up to their middle. Spurs on fore- and middle tibiae much shorter than the first tarsal segment, those on the hind tibiae not shorter than it [first tarsal segment]. Tarsal segments rather broad, slightly broadening from base to apex, hind tarsi slightly shorter than tibiae, their segments almost equal in length.

Dimensions. Body length 7.2 mm, width 3.0 mm; elytral length 4.7 mm.

Comparison. Distinguished by short, narrow prosternal process and shape of the femoral plates of hind coxae, which are highly extended laterally.

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*Possibly referring to the basal width (cf. page 92)—General Editor.

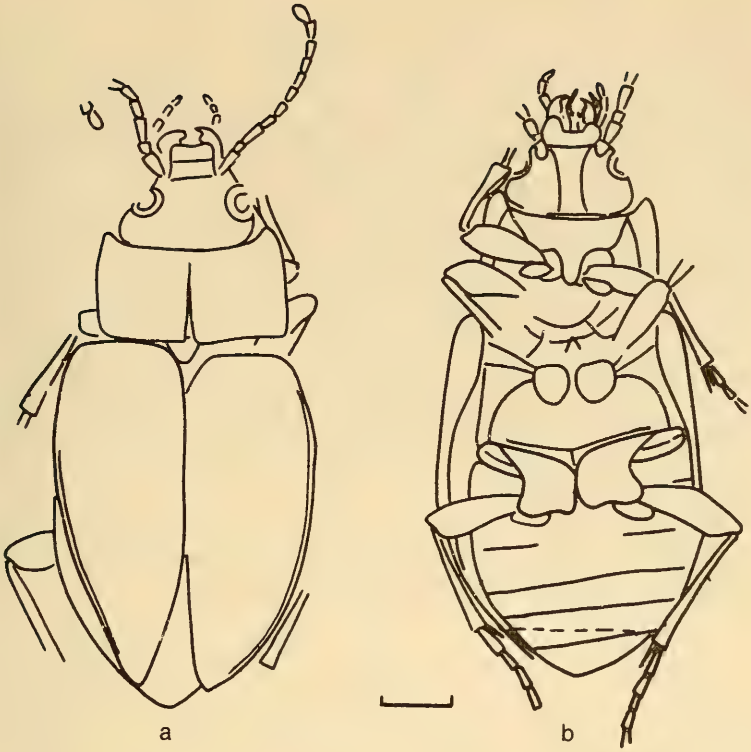

Fig. 35. *Eodromeus antiquus*, sp. nov.; holotype PIN No. 2239/897: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

Eodromeus sternalis Ponomarenko, sp. nov.
(Plate VI, Photo 2; Figure 36)

Species name coined from 'sternon' (Greek)—breast.

Holotype. No. 3191/5, PIN, impression of beetle without legs and antennae. Trans-Baikal, Chita oblast, Krasnochikoi region, well No. 102 (Chita Geological Administration, 1963), depth 138.2 m. Neocomian, Tignin series.

Material. Holotype.

Description. Head short, its length together with mandibles two-thirds the width at posterior margin, narrowing anteriorly from base. Length of temples and genae half that of eyes. Length of gular plate one-and-a-half times the medial width. Width of pronotum almost twice the length, its maximum width a little anterior middle. Prosternum scarcely shorter than pronotum, anterior to forecoxae one-and-a-half times the length [of forecoxae]. Prosternal process large, only slightly narrower than forecoxae, 69 projecting far beyond their posterior margin. Mesosternum slightly shorter than middle coxae, triangular depression wide. Mesepimera long, almost not laterally broadening. Middle coxae a little longer than wide, metasternal process between them only slightly narrower than coxae. Length of metasternum one-third the width, width at posterior margin 2.3 times that at anterior; distance between middle and hind coxae very slightly more than the length of middle coxae. Length of hind coxae sharply reduced laterally from medial fourth, further tapering gradually toward lateral margin. Length of femoral plates sharply reduced before middle of coxae [=just inside of mesal half], almost not extending laterally along the anterior margin; lateral and posterior margins very weakly emarginate. Abdomen narrowing from base of fourth sternite, width of last sternite half the abdominal base, its width 3.5 times the length. Elytra with weak but distinct grooves. Integument almost smooth, with sparse fine punctation.

Dimensions. Body length 7.1 mm, width 3.6 mm; elytral length 4.6 mm.

Comparison. Differs from other species in long prosternum, and posteriorly and laterally weakly emarginate femoral plates.

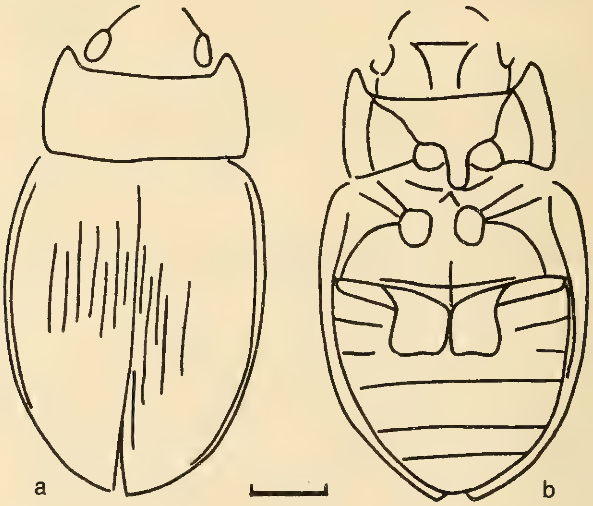

Fig. 36. *Eodromeus sternalis,* sp. nov.; holotype PIN No. 3191/5: a—dorsal view; b—ventral view . Chikoi Basin, Lower Cretaceous.

Eodromeus dissectus Ponomarenko, sp. nov.
(Plate VI, Photos 3, 4; Figure 37)

Species name coined from 'dissectus' (Latin)—cut.

Holotype. No. 1989/2967, PIN, impression of a beetle without head and pronotum. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian- Goteriv, Zazin series.

Material. Besides holotype, one impression of beetle without one antenna and major part of legs, specimen No. 3064/863* from the same site. Only the dorsal structure distinctly visible in the impression.

Description. Length of head with mandibles slightly less than its width, width of head capsule 1.7 times its length, narrowing from base anteriorly. Eyes very slightly shorter than temples, genae less than half the length of eyes. Antennae projecting beyond pronotal base by four segments; first

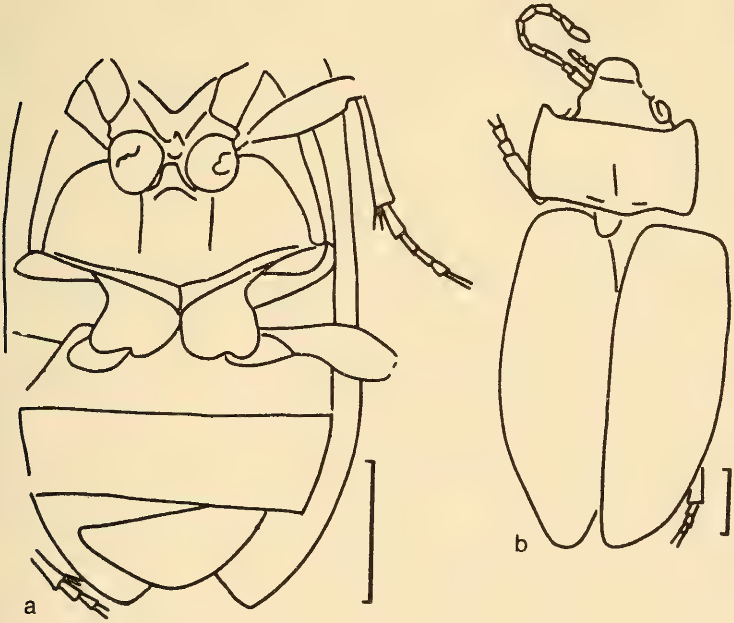

Fig. 37. *Eodromeus dissectus*, sp. nov.; a—holotype PIN No. 1989/2967; b—paratype PIN No. 3064/803. Baisa, Lower Cretaceous.

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*3064/803 in Figure legend—General Editor.

70 segment slightly thicker than flagellar segments, almost twice the length of second; third one-third longer than second; fourth and following segments subequal, two-thirds the third, only the last slightly longer. Labrum very slightly emarginate. Width of pronotum almost twice the length, anteriorly with shallow straight emargination; pronotum rounded laterally, narrowing anteriorly and posteriorly from middle, slightly protuberant at posterior margin. Anterior angles of pronotum drawn out posteriorly, blunt anteriorly. Disk of pronotum with weak transverse oval raised portion, divided by flat longitudinal groove, more distinct in posterior half. Flat lateral flange of pronotum narrow, [extreme] lateral margin not margined. Prosternum noticeably shorter than pronotum; anterior to forecoxae not shorter than them. Mesosternum rather long, only slightly shorter than middle coxae, triangular depression narrow. Length of mesopleura not less than width, pleural suture slightly oblique so that mesepisterna and mesepimera almost rectangular; mesepimera long, more than half of mesepisterna. Middle coxae round, converging, metasternal process between them less than half the coxal width. Width of metasternum at posterior margin almost three times the length posterior margin; posterior margin 2.3 times the anterior. Distance between middle and hind coxae one-and-a-half times longer than middle coxae. Longitudinal lines apparently corresponding to internal keels proceeding anteriorly along the metasternum from middle coxae backward and from hind coxae approximately to their lateral third. Metepisternum in anterior half strongly but not sharply broadened, width at anterior margin two-fifths the length. Length of hind coxae sharply reduced laterally from medial third, more laterally maintaining the same length right up to the lateral margin, length before lateral margin only two-thirds the maximum length. Femoral plates of hind coxae small, noticeably narrower than half of coxa, on anterior margin with small angular lateral projection, by far not extending to the corners of metasternum; lateral margin in anterior half with a deep emargination, roundly projecting posteriorly from it, posterior margin with a narrow and rather deep notch, postero-lateral corners somewhat extended, rounded. Abdomen weakly narrowing posteriorly from the base of third sternite; abdominal base 1.7 times as wide as last sternite; last sternite triangular, its width 1.4 times the length. Fore- and middle femora broadened uniformly, reaching maximum width almost at middle, hind femora gently clavate,widest in apical third, middle femora only slightly shorter than hind femora. Tibiae rather thick, noticeably broadening from base to apex, their outer margin with spines, length of foretibiae nearly half and middle tibiae noticeably shorter than hind tibiae; segments of foretarsi broadening, triangular, length not greater than apical width. Spurs of middle and hind tibia shorter than first tarsal segment. Middle tarsi equal to tibiae in length, basal segments broadening from base to apex, distal ones slender, almost virgate; first and last segments equal, almost twice as long as the remaining. Hind

tarsi shorter than tibiae, their segments short, first segment one-and-a-half times longer than second. Elytra smooth. Body without distinct punctation dorsally, with sparse and small punctures ventrally.

Dimensions. Body length 6.0–7.5 mm, width 2.7–3.1 mm; elytral length 4.0–5.0 mm.

Comparison. Distinguished by longer metasternum and small short femoral plates with deep emarginations and extended postero-lateral corners.

Eodromeus major Ponomarenko, sp. nov.
(Plate VI, Photo 5; Figure 38)

Species name coined from 'major' (Latin)— large.

Holotype. No. 3064/864, PIN, impression of beetle without antennae and large part of legs. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

71 *Material.* Holotype.

Description. Width of head at posterior margin 1.6 times the length of head with mandibles and 2.5 times the length of head capsule, narrowing from base anteriorly. Temples two-thirds the length of eyes, genae very short. Mandibles approximately twice as long as wide, apices incurved. Lateral

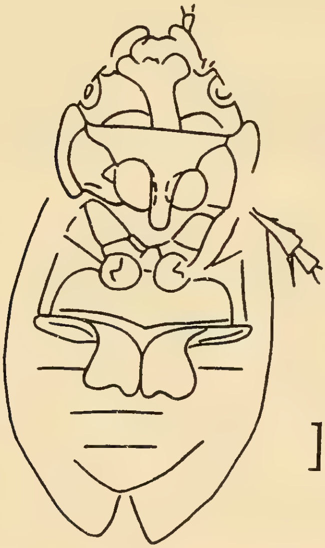


Fig. 38. *Eodromeus major*, sp. nov.; holotype PIN No. 3064/864. Basia, Lower Cretaceous.

lobes of mentum longer than wide, apically rounded. Gular plate broadening in apical third, twice as long as maximum width anterior to middle; anterior margin slightly narrower than posterior, anterior corners slightly drawn out. Prosternum slightly shorter than pronotum, anterior to forecoxae scarcely shorter than slightly transverse coxae. Prosternal process half as wide as coxae, extending slightly beyond them, rounded apically. Propleura 2.2 times longer than wide. Mesosternum equal in length to middle coxae, triangular depression equilateral. Mesopleuron distinctly less long than wide, pleural suture intersecting almost diagonally, mesepimeron strongly broadening laterally. Middle coxae oval, transverse, convergent; intercoxal metasternal process very small. Length of metasternum one-third its width at posterior margin, width at anterior margin half of posterior. Distance between middle and hind coxae one-third longer than middle coxae. Metepisternum in anterior half more strongly but not sharply broadening, its length two-and-a-half times the width. Elongate part of hind coxae narrow, not more than one-fourth their width, more laterally the coxae gradually tapering toward the lateral margin. Femoral plates of hind coxae small, at anterior margin with narrow lateral angular projection, by far not extending to metasternal corners lateral margin before the middle with deep angular emargination, posterior margin with deep emargination somewhat shifted medially from middle of posterior margin, postero-lateral corner broadly rounded. Abdomen rather strongly narrowing from the base of second sternite; width of last sternite half of abdominal base, triangular, its width 2.8 times its length. Legs short, middle femora scarcely extending beyond body margins, slightly thickened, their maximum width somewhat distal to middle. Tibiae equal in length to femora, strongly broadening in distal half, outer margin with spines, spurs not shorter than first tarsal segment. The latter almost twice as long as second segment. Metasternum with dense, small punctures, punctation of other sclerites indistinct.

Dimensions. Body length 11.3 mm, width 6.0 mm; elytral length 7.5 mm.

Comparison. Distinguished from other species by short head. Resembles *E. sternalis* in general body shape and short head, but differs in the smaller prosternal process and shape of hind coxae; resembles *E. dissectus* in the structure of hind coxae, but differs in the shorter head and metasternum.

Family CARABIDAE Latreille, 1802

Subfamily Protorabinae Ponomarenko, Subfam, Nov.

Diagnosis. Clypeus not extending up to antennal socket. Forecoxal cavities open. Lateral walls of middle coxal cavities formed by mesosternum, 72 mesepisterna, mesepimera and metasternum. Hind coxae not separating metapleuron and abdomen. Both spurs of foretibiae apical.

Composition. Five genera in the Jurassic of Soviet Central Asia and South Kazakhstan, and the Lower Cretaceous of Trans-Baikal.

Comparison. Distinguished from all other carabids by the inclusion of metepisterna into lateral walls of middle coxal cavities.

Genus *Protorabus* Ponomarenko, gen. nov.

Genus name coined from 'protos' (Greek)—first, and from genus *Carabus*.

Type species. P. planus sp. nov. Upper Jurassic of South Kazakhstan.

Description. Medium-sized, broad, flat beetles. Head triangular, transverse. Genae shorter than temples. Antennae rather long, their segments slightly broadening apically. Prosternum transverse, its maximum width anterior to middle, constricted* behind middle. Mesosternum and distance between middle and hind coxae not longer than middle coxae. Hind coxae oblique. Femoral plates laterally reaching only up to coxal middle. Abdomen short, sternites movable, apex blunt. Base of last sternite only slightly narrower than abdominal base. Legs short, femora scarcely extending beyond lateral margins of body. Elytra with grooves.

Species composition. Three species in the Upper Jurassic of South Kazakhstan.

Comparison. Distinguished by short, posteriorly weakly tapering abdomen with broad last sternite.

Protorabus planus Ponomarenko, sp. nov.
(Plate VI, Photos 6, 7; Figure 39)

Species name coined from 'planus' (Latin)—flat.

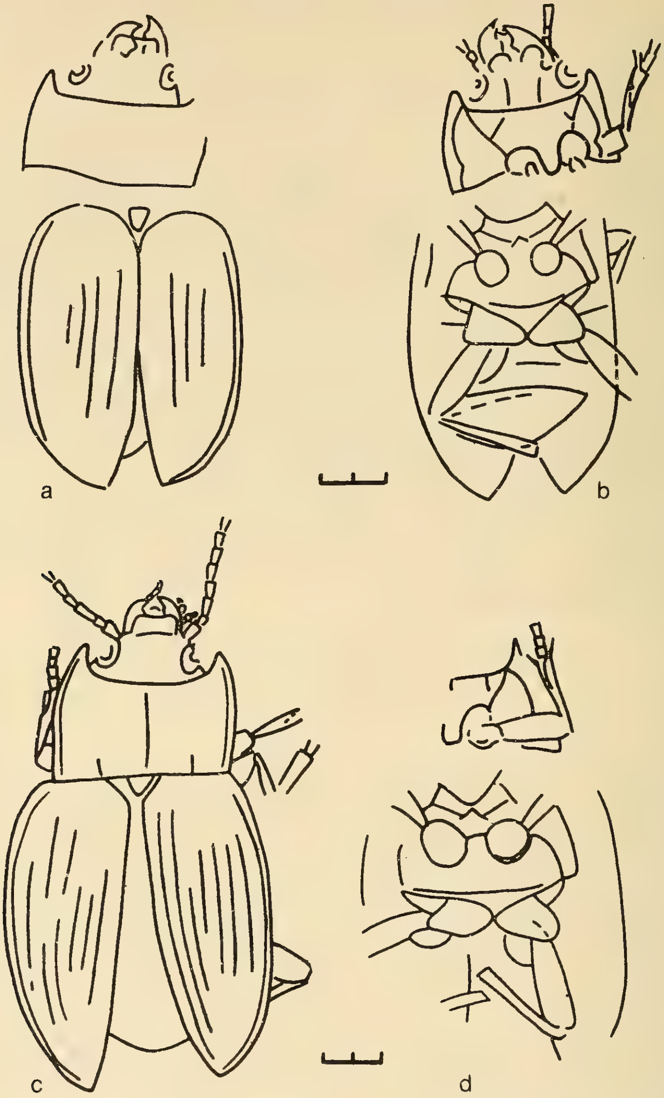
Holotype. No. 2066/3185, PIN, impression of a beetle without antennae and large part of legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, nearly entire beetles, PIN Nos. 2904/928, 2066/3187 and metathorax with abdomen, No. 2784/1299 from the same site.

Description. Head transverse, triangular, head capsule almost half its width at posterior margin, uniformly narrowing anteriorly from base. Temples shorter than eyes and longer than genae. Labrum weakly emarginate at apex. Mandibles almost equal to head capsule in length. Submental lobes

*The Russian original reads 'behind middle prosternum', which makes no sense. A comparison with the generic descriptions of *Cordorabus* and *Cretorabus* on subsequent pages, suggests that the word 'perednegrud' (= prosternum) was accidentally substituted for the word 'peretyanuta' (= constricted)—Scientific Editor.

narrow, incision between them rather deep. Antennae projecting far beyond pronotal base, their first segment noticeably thickened, second equal in length and width, third equal to first and second together, remaining flagellar



73 Fig. 39. *Protorabus planus*, sp. nov.; a, b—holotype PIN No. 2066/3185: a—dorsal view; b—ventral view; c, d—paratype PIN No. 2904/928: c—dorsal view, d—ventral view. Karatau, Upper Jurassic.

segments equal, two-thirds the length of third. Pronotum noticeably longer than head, its length two-thirds the basal width, anterior margin with shallow rounded emargination. Pronotum margined laterally, posterior margin with longitudinal groove. Prosternum noticeably shorter than pronotum, anterior to forecoxae approximately as long as forecoxae. Prosternal process half as wide as coxae straight, short, scarcely extending beyond coxae. Propleura almost twice as long as wide. Mesosternum shorter than middle coxae, with triangular depression for prosternal process, mesepisterna almost square, mesepimera short, laterally almost not widening. Length of metasternum approximately one-fourth the width at posterior margin, anterior margin approximately half the width of posterior; distance between [middle and hind] coxae noticeably shorter than middle coxae. Posterior margin of metasternum angularly projecting, distance from apex of angle to transverse metasternal suture only slightly shorter than hind coxae. Hind coxae laterally tapering, triangular, femoral plates wider than long, angularly extending
73 posteriorly and laterally. Metepisterna sharply broadening in front of anterior margin, width at anterior margin half the length, posterior margin rather wide; metepimera mesally not broadening. In impressions, abdomen only slightly longer than meso- and metathorax together, narrowing from base of penultimate sternite, length of last sternite one-third the basal width. Femora not strongly but uniformly thickened, tibiae flat, broadening from base to apex. Foretibiae slightly shorter than femora, on inner side with groove for cleaning antennae and small notch preapically. Apical spurs shorter than primary tarsal segments. Four basal segments of foretarsi broadening toward apex, scarcely longer than their width. Hind tibiae almost linear, broadening only preapically, not shorter than femora. Furrows of elytra wide, flat, indistinct. Integument with small, sparse punctation.

Dimensions. Body length 14.7–16.0 mm, width 6.7–8.3 mm; elytral length 8.6–9.7 mm.

Comparison. Distinguished by longer pronotum and more sharply anteriorly narrowing metasternum.

74 *Protorabus nigrimonticola* Ponomarenko sp. nov.

(Plate VI, Photo 8; Figure 40)

Species name coined from ‘nigrimonticola’ (Latin)—inhabitant of Black mountains (Karatau).

Holotype. No. 2997/1851, PIN, impression of an almost entire beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, one impression of beetle without legs, No. 2997/485, two impressions of metathorax and abdomen, specimen Nos. 2997/1866 and 2066/2531 from the same site.

Description. Head including mandibles almost equal in length and width, triangular, head capsule two-thirds its basal width, uniformly narrowing from base anteriorly. Temples less than two-thirds the eyes, genae shorter than temples. Apex of labrum truncated. Submental lobes rather broad, anteriorly rounded. Antennae projecting far beyond pronotal base; their first segment thickened, equal in length to second and third together; second small, almost equal in length and width, half the length of third; third noticeably longer than fourth; remaining flagellar segments equal in length. Pronotum scarcely longer than head, almost half the basal width, anterior margin with rather deep rounded emargination, laterally widely margined. Prosternum much shorter than pronotum, prosternum anterior to forecoxae shorter than them. Prosternal process half the forecoxae in width, straight, noticeably extending beyond their posterior margin. Mesosternum shorter than middle coxae, anteriorly with triangular depression for prosternal process, mesepisterna transverse, mesepimera short, noticeably broadening laterally. Metasternum almost one-third the width of posterior margin, anterior margin half the width of posterior, distance between middle and hind

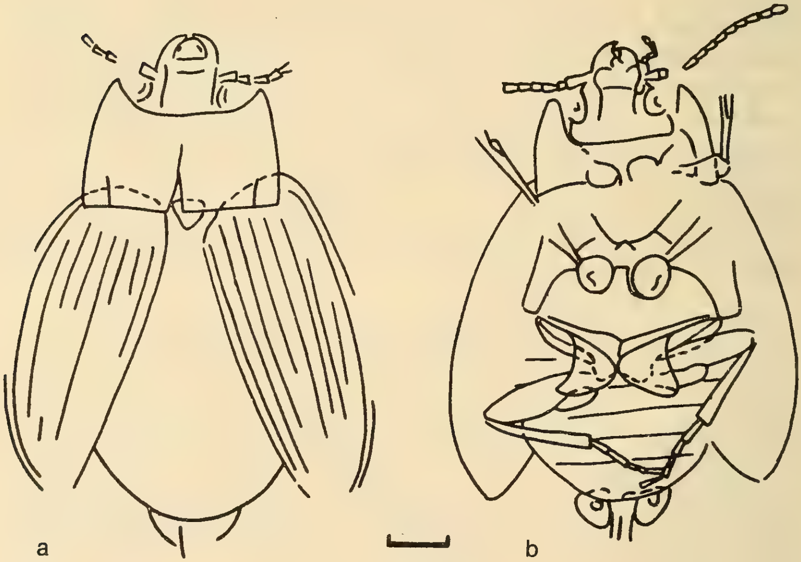


Fig 40. *Protorabus nigrimonticola*, sp. nov.; holotype PIN No. 2997/1851: a—dorsal view; b—ventral view. Karatau, Upper Jurassic.

coxae slightly longer than midcoxae. Hind margin of metasternum and transverse metasternal suture angularly extending posteriorly, distance between them much shorter than hind coxae. Hind coxae triangular, femoral plates almost equal in length and width, coxae 2.3 times longer than femoral plates. Metepisterna gradually broadening anteriorly almost from posterior margin, width at anterior margin half the length. Abdomen noticeably longer than meso- and metathorax together, narrowing posteriorly almost from base, length of last sternite three-fourths its basal width. Femora weakly but
75 uniformly thick, foretibiae shorter than femora, almost not broadening toward apex, inner side with groove and apical third with notch for cleaning antennae. Hind tibiae slightly broadening from base to apex; hind tarsi shorter than tibiae, their first segment longer, almost equal to third and fourth together; second noticeably shorter than first*, equal to fifth segment. Integument with fine, sparse punctation. Grooves on elytra rather deep and sharp.

Dimensions. Body length 7.6–8.8 mm, width 3.8–4.6 mm; elytral length 5.2–6.0 mm.

Comparison. Distinguished by shorter pronotum, longer and less sharply anteriorly narrowing metasternum, and angular transverse metasternal suture.

Protorabus magnus, Ponomarenko, sp. nov.
(Plate VI, Photo 9; Figure 41)

Species name coined from 'magnus' (Latin)—large.

Holotype. No. 2554/447, PIN, impression of metasternum, abdomen and hind legs of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Length of mestasternum two-fifths the width at posterior margin, width at posterior margin 1.7 times that at anterior. Posterior margin of metasternum angularly projecting backward, transverse metasternal suture straight; distance between apex of angle and transverse suture half the length of hind coxae. Hind coxae triangular, femoral plates equal in length and width, half the coxal width, laterally strongly emarginate. Metepisterna sharply broadening in anterior third, angularly tapering at posterior margin. Abdomen narrowing from fourth sternite, length of last sternite one-third the basal width. Hind femora clavate, widest in distal third, tibiae linear, equal to femora in length, tarsi noticeably shorter, first segment one-and-a-half times longer than second, second to fourth equal, noticeably broadening

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*In the Russian original words from tibiae (line 2 from top) to 'shorter than' (line 4 top) repeated, which have been deleted here—General Editor.

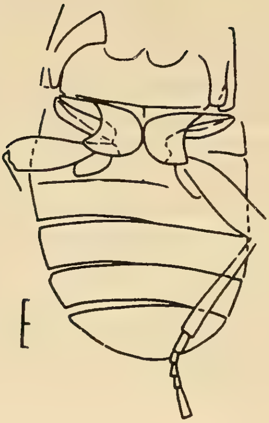

Fig. 41.* *Protorabus magnus* sp. nov.; holotype PIN No. 2554/447. Karatau, Upper Jurassic.

apically, last equal to the preceding two together. Integument with small, dense punctation.

Dimensions. Length of fragment 15 mm, width 11 mm; length of beetle apparently about 20 mm.

Comparison. Distinguished by long metasternum, posteriorly narrowing metepisterna and long terminal abdominal sternite.

76 Genus *Ovrabites* Ponomarenko, gen. nov.

Genus name coined from 'ovum' (Latin)—egg.

Type species. *O. ovalis* sp. nov. Upper Jurassic of South Kazakhstan.

Description. Small, oval, flat beetles. Head triangular, approximately equal in length and width. Antennae long, their segments slightly apically broadening. Prosternum transverse, trapezoidal, maximum width at base. Prosternal process broadening toward apex, apically truncate. Mesosternum with a triangular depression for prosternal process. Hind coxae oblique, length of femoral plates reduced laterally, plates much narrower than hind coxae. Abdomen rather long, posteriorly narrowing almost from base; base of the last abdominal sternite much narrower than remaining sternites, width half the abdominal base, apex of abdomen rather pointed. Legs short, femora scarcely extending beyond body margins. Elytra smooth.

Species composition. Two species in the Late Jurassic of South Kazakhstan.

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*This figure was printed upside down in the Russian original—General Editor.

Comparison. Differs from all other genera in the shape of pronotum—widest at base and uniformly tapering anteriorly.

Ovrabites ovalis Ponomarenko, sp. nov.
(Plate VII, Photo 1; Figure 42)

Species name coined from 'ovalis' (Latin)—egg-shaped.

Holotype. No. 2904/872, PIN, impression of beetle without large part of legs; South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

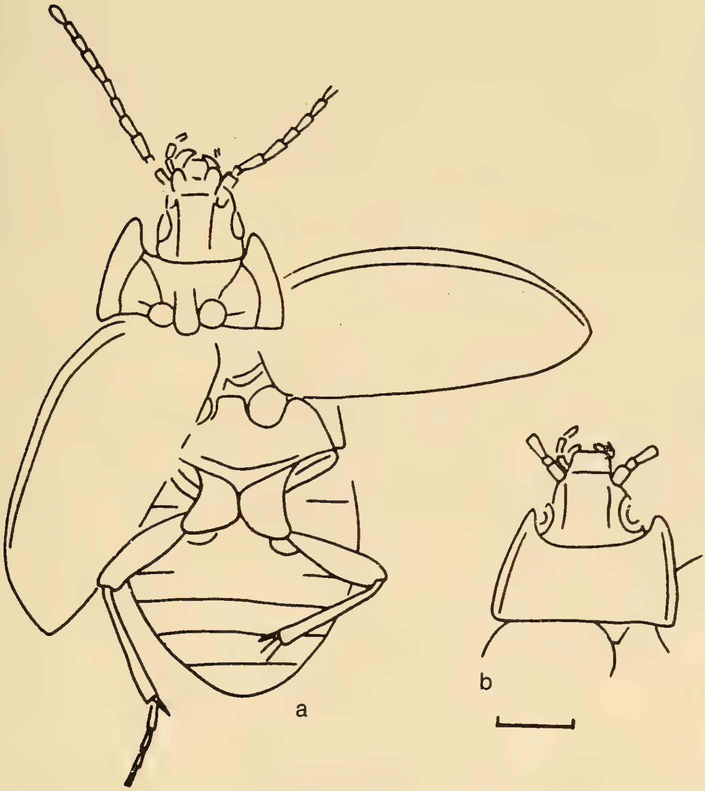


Fig. 42. *Ovrabites ovalis*, sp. nov.; holotype PIN No. 2904/872: a—ventral view; b—dorsal view of head, and pronotum. Karatau, Upper Jurassic.

77 *Material.* Holotype and almost entire impressions of beetles, specimen Nos. 2384/554, 2904/875, 2554/526, 2784/1326 from the same site.

Description. Head including mandibles very slightly shorter than its basal width, uniformly tapering from base anteriorly.Temple and genae very short, much shorter than eyes. Labrum truncate. Mandibles half the length of head capsule. Submental lobes rather wide, apically rounded. Antennae projecting by one-third beyond pronotal base. Their first segment thicker than remaining segments, half of third; second cylindrical, equal in length and width, half the length of third; third and fourth slightly longer than the remaining flagellar segments. Pronotum almost same length as head, approximately half its basal width; anterior margin with deep, almost rectangular emargination; posterior margin weakly angularly projecting backward; laterally margined. Prosternum only slightly shorter than pronotum, anterior to forecoxae noticeably longer than them. Prosternal process slightly narrower than coxae. Propleura twice as long as wide. Mesosternum very short, almost taenioid, half the length of middle coxae. Length of metasternum one-third its width at posterior margin; width at posterior margin 1.8 times that at the anterior; distance between middle and hind coxae almost equal to length of middle coxae. Posterior margin of metasternum angularly projecting, transverse metasternal suture posteriorly weakly convex, distance between it and apex of angle at hind margin less than half the length of hind coxae. Hind coxae nearly same length, noticeably shorter than femoral plates. Femoral plates longer than width at anterior margin, basal margin emarginate, postero-lateral angles acute, extended. Metepisterna sharply broadening in front of anterior end. Abdomen twice as long as meso- and metathorax together, narrowing almost from base; last sternite very slightly longer than penultimate, its basal width 3.5 times the length. Fore- and middle femora slightly thickened, hind femora considerably thickened. Tibiae slender, scarcely broadening toward apex, middle tibiae shorter than femora, hind tibiae very slightly longer. Hind tarsi slender, linear, their segments almost equal in length, scarcely broadening toward apex. Integument with fine and rather dense punctation.

Dimensions. Body length 6.2–7.2 mm, width 2.7–3.0 mm; elytral length 4.0–4.8 mm.

Comparison. Distinguished by shorter metasternum.

Ovrabites jurassicus Ponomarenko, sp. nov.
(Plate VII, Photo 2; Figure 43)

Holotype. No. 2904/877, PIN, impression of beetle without legs and apices of antennae. South Kazakhstan, Chimkent oblast, Algabass region, southwestern flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Besides holotype, impression of beetles without legs, specimen No. 2997/407 from the same site, and No. 2452/33 from the Karatau-Galkino site.

Description. Head triangular, noticeably shorter than its basal width, narrowing from posterior margin of eyes anteriorly. Temples noticeably longer than genae, two-thirds of eyes. Labrum truncate. Mandibles short, half the length of head capsule. Submental lobes small, apically rounded. Antennae extending beyond pronotal base by half their length. Their third segment is equal to the first and second together, scarcely thinner than the first; fourth noticeably shorter than third; remaining flagellar segments equal to fourth segment. Pronotum noticeably longer than head, half the basal width; anterior margin with rather deep rounded emargination, posterior margin almost straight, prosternum slightly shorter than pronotum, anterior to forecoxae shorter than them. Prosternal process scarcely projecting beyond coxae, slightly narrower than them. Length of propleura two-thirds the maximum width. Mesosternum two-thirds the length of middle coxae. Length of metasternum two-fifths the basal width, width at anterior margin 78 approximately half that posterior. Distance between middle and hind coxae much longer than middle coxae. Posterior margin of metasternum angular, transverse metasternal suture roundly projecting posteriorly. Distance between them half the hind coxae. Length of hind coxae sharply reduced laterally from medial third, length gradually decreasing further on, their

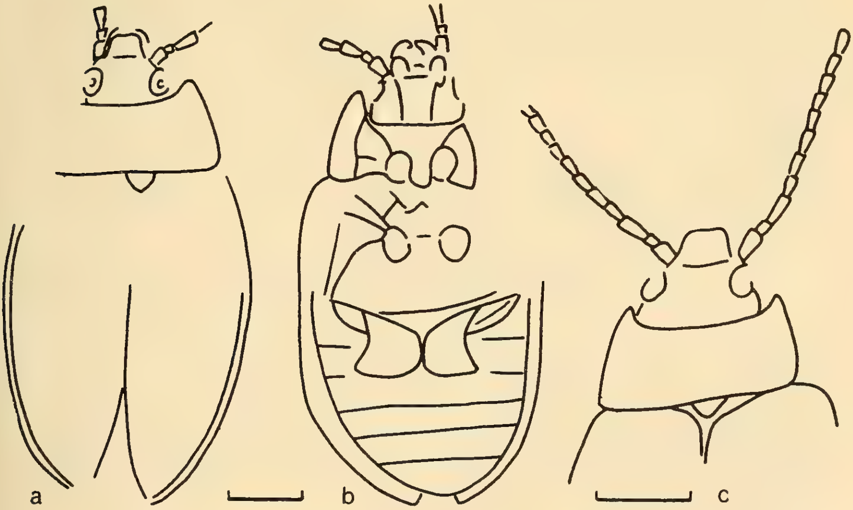


Fig. 43. *Ovrabites jurassicus*, sp. nov.; a, b—holotype PIN No. 2904/877: a—dorsal view, b—ventral view; c—paratype PIN No. 2452/83. Karatau, Upper Jurassic.

raised part just slightly less than femoral plate in length. Length of femoral plate equal to width at anterior margin, lateral margin strongly emarginate, postero-lateral angles acute, extended. Metepisterna broadening from middle anteriorly. Abdomen one-and-a-half times longer than meso- and metathorax together, tapering almost from base; last sternite not longer than penultimate, almost one-fourth the basal width. Integument with fine, rather dense punctation.

Dimensions. Body length 5.9–6.4 mm, width 3.0–3.2 mm; elytral length 4.2–4.4 mm.

Comparison. Distinguished by longer metasternum, less sharply narrowing anteriorly.

Genus *Cordorabus* Ponomarenko, gen. nov.

Genus name coined from 'cor' (Latin)—heart.

Type species. C. notatus sp. nov. Upper Jurassic of South Kazakhstan.

Description. Small, cylindrical beetles. Head triangular, transverse. Eyes somewhat shifted dorsally. Antennae slender, projecting a little beyond pronotal base, their segments almost not apically broadening. Prosternum transverse, widest anterior to middle, behind it slighly constricted. Prosternal process noticeably narrower than forecoxae. Mesosternum half the length of middle coxae, with triangular depression for prosternal process at middle. Hind coxae, oblique, femoral plates laterally reduced, scarcely projecting into lateral half of coxa, laterally not emarginate. Abdomen rather long, posteriorly tapering almost from base, apex pointed. Legs short, femora scarcely extending beyond lateral body margins. Tarsi long, slender. Elytra smooth.

Species composition. Three species in the Late Jurassic of South Kazakhstan.

Comparison. Resembles *Protorabus* in the shape of pronotum, but differs in pointed abdomen and smooth elytra.

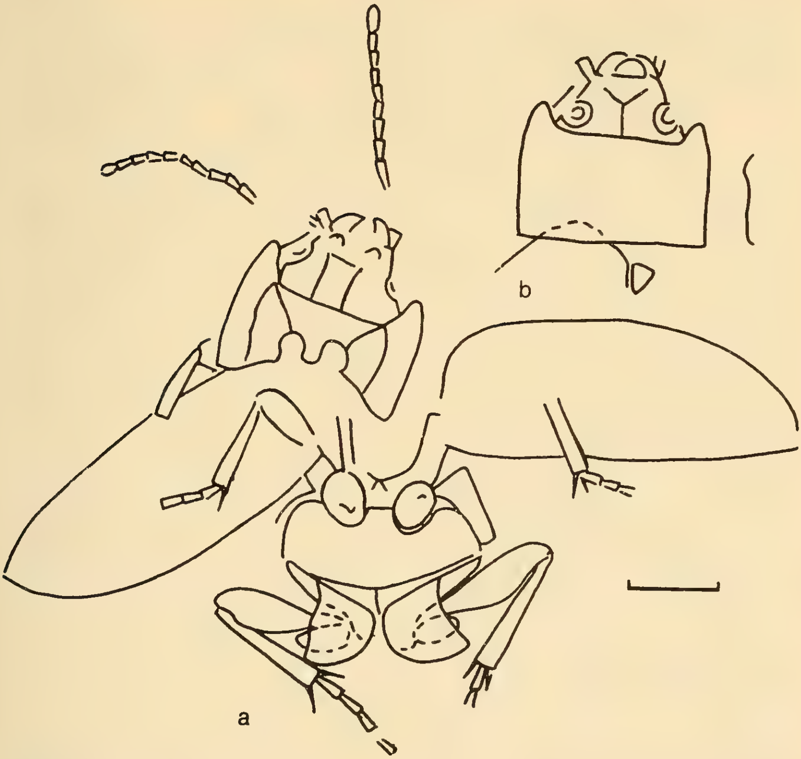
79 *Cordorabus notatus* Ponomarenko, sp. nov.
(Plate VII, Photo 3; Figure 44)

Species name coined from 'noton' (Greek)—back.

Holotype. No. 2066/2739, PIN, impression of a beetle without abdomen. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype and almost entire impressions of beetles, PIN Nos. 2066/2879, 2784/1320, 2997/534, 2997/1867 from the same site.

Description. Head noticeably shorter than its basal width, anteriorly narrowing, retracted under pronotum almost up to eyes. Temples slightly longer than genae, almost equal to eyes in length. Labrum apically emarginate. Mandibles rather short, blunt, two-thirds the length of head capsule. Antennae extending beyond pronotal base by only three segments. First antennal segment shorter and almost not thicker than third, third 1.3 times longer than fourth, remaining flagellar segments almost equal. Pronotum longer than head, length two-thirds the width at posterior margin, anterior margin with shallow rounded emargination, posterior margin straight. Prosternum approximately half the length of pronotum, in front of forecoxae slightly shorter than them. Prosternal process almost not extending beyond forecoxae. Length of propleuron twice its maximum width. Width of metasternum at posterior margin 3.5 times its length, width at anterior margin half that at posterior. Distance between middle and hind coxae scarcely



80 Fig. 44. *Cordorabus notatus*, sp. nov.; holotype PIN No. 2066/2739: a—ventral view; b—dorsal view of head, and pronotum. Upper Jurassic.

longer than middle coxae. Posterior margin of metasternum angular, transverse metasternal suture roundly projecting posteriorly; distance between the angle and transverse suture one-third the length of hind coxae. Hind coxae laterally reduced [tapering] right up to lateral margins, approximately half the length of femoral plates, their posterior margins forming rather smooth curve. Length of femoral plates equal to width at anterior margin, anteriorly and at postero-lateral corners extended laterally, lateral margin slightly protuberant medially. Metepisterna sharply broadening in

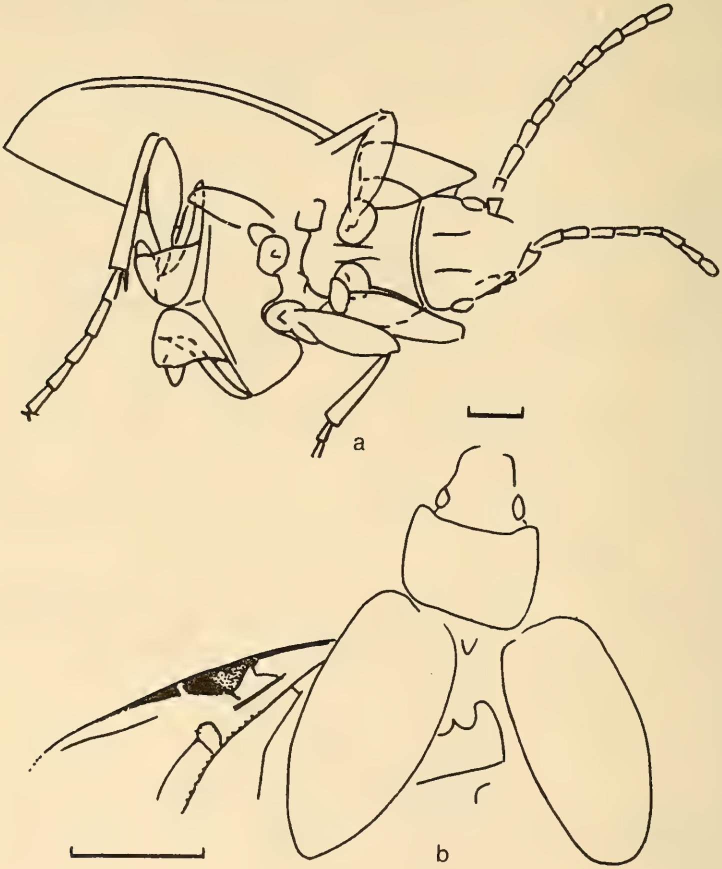


Fig. 45. Representatives of genus *Cordorabus*: a—*C. antennatus*, sp. nov.; holotype PIN No. 2066/2363; b—*C. minimus*, sp. nov.; holotype PIN No. 2239/905. Karatau, Upper Jurassic.

front of anterior margin. Fore- and middle femora uniformly thickened, hind femora clavate; fore- and middle femora almost equal in length, hind femora slightly longer. Foretibiae noticeably and middle tibiae slightly shorter than but hind tibiae equal to [corresponding] femora. Foretibiae with longitudinal groove for cleaning antennae, apical spurs stiff, slightly shorter than first tarsal segment. First segment of hind tarsus longer than remaining segments, fourth shortest. Integument with fine, dense punctation.

Dimensions. Body length 6.1–6.5 mm, width 2.7–3.0 mm; elytral length 3.8–4.2 mm.

Comparison. Distinguished by shorter antennae, shorter prosternum and head, and shape of femoral plates.

Cordorabus antennatus Ponomarenko, sp. nov.
(Plate VII, Photo 4; Figure 45a)

Species name coined from 'antenna' (Latin)—antenna, feeler.

Holotype. No. 2066/2363, PIN, impression of a beetle without abdomen. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

81 *Material.* Holotype.

Description. Head scarcely shorter than its basal width, retracted up to eyes under pronotum. Temples slightly shorter than eyes, genae very short, antennae attached near anterior margin of eyes. Antennae projecting beyond pronotal base by four segments. First antennal segment thickened, not longer than fourth, shorter than third which is longer than first and second together; third longer than fourth; remaining flagellar segments almost equal. Pronotum very slightly longer than head, approximately half the basal width, anterior margin with shallow, almost rectangular emargination. Prosternum anterior to forecoxae slightly longer than them, prosternal process much narrower than forecoxae, noticeably broadening posteriorly. Length of propleuron two-and-a-half times its maximum width. Length of metasternum one-third its basal width, posterior margin 1.7 times of anterior. Distance between middle and hind coxae very slightly larger than diameter of the former. Metepisterna sharply broadening in front of anterior margin. Hind coxae rather sharply tapered beyond medial fourth, further on almost untapered right up to lateral margins. Femoral plates slightly shorter than width at anterior margin, markedly extending laterally beyond anterior margin, postero-lateral corners almost right-angled, lateral margin scarcely distinctly protuberant. Fore- and middle femora equal in length, hind femora one-third longer, fore-femora uniformly thickened almost along entire length, middle femora thickest just slightly distal to middle, and hind femora slightly proximal to middle. Middle and hind tibiae equal in length to femora, not strongly broadening from base to apex, apical spurs much shorter than basal tarsal segment. Hind tibiae equal in length to four hind tarsal segments, first two segments slightly longer than the subequal remaining segments. Body with rather fine punctation, punctures noticeably larger only on metasternum.

Dimensions. Body length 9.4 mm, width 4.3 mm; elytral length 6.2 mm.

Comparison. Distinguished by longer antennae, prosternum and head, and shape of femoral plates.

Cordorabus minimus Ponomarenko, sp. nov.
(Plate VII, Photo 5; Figure 45b)

Species name coined from 'minimus' (Latin)—smallest.

Holotype. No. 2239/905, PIN, impression of a beetle without antennae and legs, with unfolded wing. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head slightly shorter than its basal width. Temples slightly shorter than eyes, genae half their length. Pronotum equal to head in length, its basal width 1.3 times the length, widest in anterior third, posteriorly roundly narrowing, not broadening in front of posterior corners, anterior margin with shallow rounded emargination. Length of metasternum approximately one-third the width at posterior margin, width at anterior margin half of that of posterior; distance between middle and hind coxae slightly longer than the former. Metepisterna gradually broadening anteriorly from middle. Hind coxae laterally short*. Femoral plates equal in length and width. Wing with very large pterostigma, "oblongum" rather wide at anterior margin. Body with fine sparse punctation.

Dimensions. Body length 4.8 mm, width 2.8 mm; elytral length 3.2 mm.

Comparison. Differs from other species in long narrow pronotum which is narrowest at posterior margin.

Remarks. The species is described from a single, rather poorly preserved specimen, and hence its inclusion in this genus is not wholly reliable.

82 Genus *Lithorabus* Ponomarenko, gen. nov.

Genus name coined from 'lithos' (Greek)—stone, and genus *Carabus*.

Type species. L. incertus, sp. nov. Lower Jurassic of Soviet Central Asia.

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*So given in the Russian original. By context it should read 'laterally reduced'—General Editor.

Diagnosis. Small, flat beetles. Metasternum longer than middle coxae. Hind coxae almost transverse, their anterior margin somewhat slanting backward only mesally. Length of femoral plates laterally reduced but extending to lateral margins of coxae, their midcoxal length is not less than half the maximum length. Elytra with shallow flat grooves.

Species composition. Monotype genus.

Comparison. Distinguished from other genera by the shape of femoral plates which are very slightly reduced laterally. Differs from *Cretorabus*, in which the femoral plates also extend to lateral margins of coxae, but blunt posterior corner of metepisternum without mesal process.

Lithorabus incertus Ponomarenko, sp. nov.
(Plate VII, Photo 6; Figure 46)

Species name coined from 'incertus' (Latin)—uncertain.

Holotype. No. 371/49, PIN, impression of metasternum and elytra of beetle, Kirgiz SSR, Tonsk region, southern shore of Issyk-Kyl' lake, cost of Kazhdi-Sai settlement (Issyk-Kul' site). Lower Jurassic, Dzhil' series.

Material. Holotype.

Description. Middle coxae large, contiguous, slightly elongate. Length of metasternum two-fifths the width of posterior margin, width at posterior margin 1.7 times that of anterior. Distance between middle and hind coxae slightly longer than the former. Posterior margin of metasternum extending backward at middle as a sharp tongue-like process; transverse metasternal

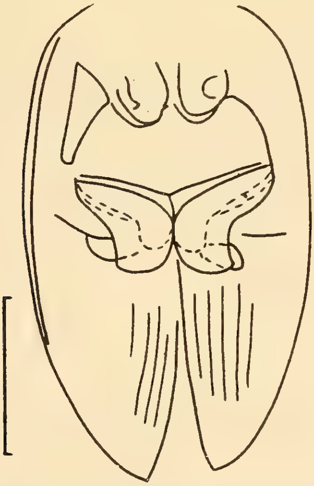


Fig. 46. *Lithorabus incertus*, sp. nov.; holotype PIN No. 371/49. Issyk-Kul'. Lower Jurassic.

suture angularly projecting backward. Width of hind coxae 1.8 times the length, sharply reduced beyond mesal third, and gradually reduced further laterally. Femoral plates slightly shorter than wide, reduced near coxal middle by approximately half, and gradually reduced more laterally, longer than coxa at lateral margin, postero-lateral corners of the elongate part of femoral plates noticeably extending. Metepisterna broadening anteriorly from posterior margin, their posterior margin truncate. Grooves on elytra indistinct, those near the suture proceeding along the suture up to elytral apex, more lateral grooves reduced in length. Metasternum almost smooth.

Dimensions. Body length about 5 mm, width 1.8 mm; elytral length 3.1 mm.

83 Genus *Cretorabus* Ponomarenko, gen. nov.

Genus name coined from 'creta' (Latin)—chalk, and genus *Carabus*.

Type species. C. capitatus, sp. nov., Lower Cretaceous of Trans-Baikal.

Description. Small and medium-sized, broad, flattened beetles. Head large, strongly transverse. Eyes convex, genae very short, antennae rather short, with thick segments. Pronotum transverse, maximum width anterior to middle, constricted behind middle. Meso- and metasterna long, latter much longer than middle coxae. Metepisterna posteriorly tapering. Hind coxae almost straight, their anterior margin slanted backward only in middle part of the body. Length of femoral plates sharply reduced in lateral half, extending to lateral margins of hind coxae by narrow angular tongue, femoral plates laterally shorter than coxae. Abdomen short, apex rounded, last sternite distinctly longer than remaining sternites, its basal width approximately two-thirds of abdominal base. Legs short, femoral apices slightly extending beyond lateral body margins. Elytra smooth or with numerous rows of large punctures fusing into longitudinal meandering grooves.

Species composition. Two species in Early Cretaceous of Trans-Baikal.

Comparison. Distinguished from other genera by the shape of femoral plates whose length is sharply reduced laterally but extending to sides of coxae; differs from *Lithorabus* by posteriorly tapering metepisterna.

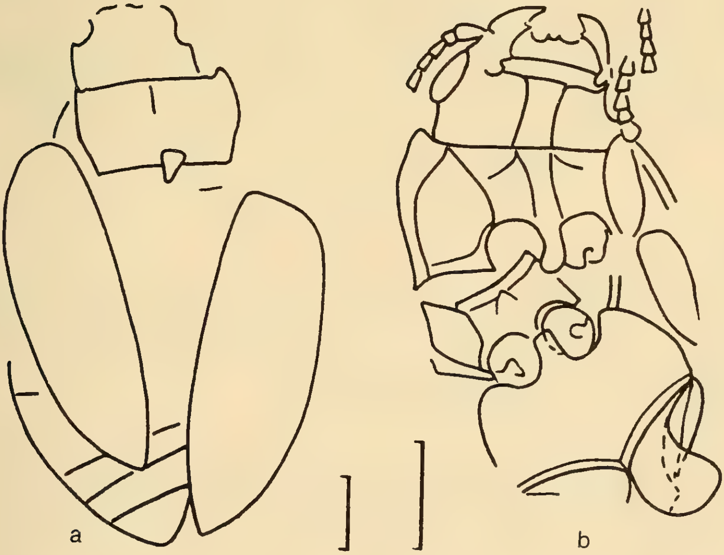
Cretorabus capitatus Ponomarenko, sp. nov.
(Plate VII, Photo 7; Figure 47)

Species name coined from 'capitatus' (Latin)—large headed.

Holotype. No. 3064/862, PIN, impression of a beetle with displaced sclerites, distal parts of legs and tip of abdomen absent. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Small beetle with flattened body. Length of head two-thirds its width, untapered all the way to anterior margin of eyes. Eyes large, strongly protruding, longer than temples. Mandibles short, blunt. Gular plate twice as long as wide, slightly narrowing at middle, much narrower than submentum, submentum shorter than mentum, lateral lobes of mentum short. Antennae extending only up to base of pronotum, their segments almost cylindrical, proximal segments one-and-a-half times longer than their width, distal segments scarcely longer than wide. First antennal segment narrower than distal flagellar segments, longer than third; third same as fourth in size; flagellar segments equal in length; apical segment almost spherical. Width of pronotum 1.8 times its length, same length as head and only a little wider than it, slightly narrowing anteriorly in anterior third, constricted in posterior third, anterior and posterior angles acute, prolonged. Anterior margin of pronotum very weakly roundly emarginate at middle, at anterior angles with small, rather deep recess, lateral margin margined, longitudinal grooves passing through middle of disk. Prosternum in front of forecoxae almost one-and-a-half times longer than them; prosternal process small, two-fifths of coxae in width; anteriorly extending on prosternum as flat projection,



84 Fig. 47. *Cretorabus capitatus*, sp. nov.; holotype PIN No. 3064/862: a—dorsal view; b—ventral view of head and thorax. Baisa, Lower Cretaceous.

laterally bounded by sharp planes; oblique raised lines proceeding laterally and posteriorly from the anterior corners of this projection to the pleura. Propleura wide, slightly narrowing anteriorly, one-and-a-half times longer than wide. Forecoxae rounded. Mesosternum only slightly shorter than middle coxae, mesepisterna broad, rhomboidal, mesepimera short, taenioid, slightly broadening laterally. Middle coxae larger, rounded, contiguous under united processes and meso- and metasterna. Scutellum triangular. 84 Length of metasternum less than its width at posterior margin, anterior margin half the width of posterior; distance between middle and hind coxae one-and-a-half times large than middle coxae. Posterior margin of metasternum projecting from middle backward at acute angle. Length of hind coxae two-thirds the width, laterally slightly reduced, lateral margin half the medial, raised part only a little shorter than femoral plate. Length of femoral plate two-thirds the coxal width, its projection rounded posteriorly, posterolateral corner not strongly extending, lateral margin emarginate. Abdomen one-and-a-half times longer than meso- and metathorax together, sutures between basal sternites faint, three posterior most sternites shorter than basal sternites. Femora short and broad, approximately twice as long as wide, hind femora clavate. Tibiae scarcely broadening toward apex, shorter than femora, foretibiae with groove and anteriorly broadening apex forming apparatus for cleaning antennae, hind tibiae preapically with spines and longitudinal band. Elytra almost smooth with indistinct interweaving longitudinal rows of punctures. Punctation fine and weak.

Dimensions. Body length 7.3 mm, width 3.1 mm; elytral length 4.2 mm.

Comparison. Distinguished by less wide body, longer metasternum and smaller size.

Cretorabus latus Ponomarenko, sp. nov.
(Plate VII, Photo 8; Figure 48)

Species name coined from 'latus' (Latin)—broad.

Holotype. No. 3064/852, PIN, impression of metasternum, abdomen and elytra of a beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Rather large beetle. Length of metasternum one-third the width at posterior margin; distance between middle and hind coxae only slightly longer than middle coxae. Posterior margin of metasternum projecting backward at acute angle. Mesepisternum wide, slightly broadening in anterior half, sharply tapering in front of posterior end and with narrow angular tongue directed posteriorly and mesally toward lateral corners of hind coxae. Narrow tongue of mesepimeron also reaching this point. Possibly

85 the posterior projections of the metapleurites were actually internal and were not visible externally in the beetle. Width of hind coxae 1.8 times their length, their length laterally rather strongly reduced, lateral margin one-third the mesal, projecting part of coxa slightly shorter than femoral plate. Width of coxa 1.3 times that of femoral plate; its projecting part rounded posteriorly and laterally, lateral margin almost without emargination. Sutures between three basal sternites of abdomen noticeable only laterally, last sternite longer than remaining sternites, its length one-third the width. Elytra with longitudinal rows of large punctures. Punctation rather coarse and dense, particularly on metasternum.

Dimensions. Body length about 15 mm, width 7 mm; elytral length 9.8 mm.

Comparison. Distinguished by broad body and short metasternum.

CARABIDAE INCERTAE SEDIS

Tribe CONJUNCTIINI Ponomarenko, trib. nov.

Diagnosis. Clypeus not extending to antennal socket. Forecoxal cavities closed. Meso- and metasterna contiguous lateral to middle coxae, mesopleura not extending to their cavities. Hind coxae not dividing metapleura and abdomen, metepisterna with mesal process. Both spurs of foretibiae apical.

Composition. Two genera in the Mesozoic of Asia: *Mesorabus* in the Late Jurassic of South Kazakhstan, and *Conjunctia* in the Early Cretaceous of Trans-Baikal.

Comparison. Distinguished from other beetles by the apical position of both spurs of foretibiae and closed middle coxal cavities.

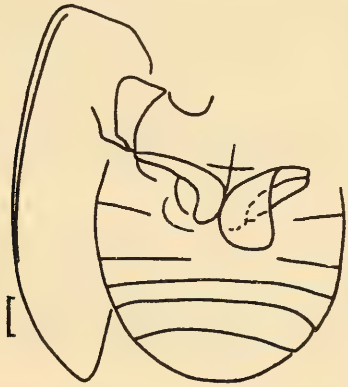


Fig. 48. *Cretorabus latus*, sp. nov.; holotype PIN No. 3064/852. Baisa, Lower Cretaceous.

Remarks. In the fossil material it is very difficult to ascertain the position of the depression for cleaning the antennae. Both spurs of foretibiae are apical, but we cannot entirely rule out the possibility that the groove for cleaning the antennae passes between them as in *Cychrus*. It is consequently also impossible to unequivocally state whether the described group belongs to Isochaeta or Simplicia. Judging from the character of the inner margin of tibia in *Conjunctia* and mesepisterna with mesal process, it is more probably affiliated to Isochaeta. In any case, based on the structure of foretibiae this group belongs to the most primitive [carabids], while on the basis of the structure of pro- and mesosterna it can be included among the most advanced carabids.

Genus *Mesorabus* Ponomarenko, gen. nov.

Genus name coined from 'mesos' (Greek)—middle, and genus *Carabus*.

Type species. M. elongatus, sp. nov. Upper Jurassic of South Kazakhstan.

Description. Rather large, elongate, cylindrical beetles with large projecting mandibles. Head large, slightly tapering anteriorly. Genae shorter than temples. Gular plates narrow. Antennae with short monoliform segments. Mandibles large, asymmetric. Pronotum shorter than head, transverse, slightly constricted anterior to the base. Propleura longer than wide. Prosternal 86 process narrow, apically rounded. Mesosternum longer than middle coxae, metasternum rather long, slightly tapering anteriorly, its posterior margin almost straight, transverse suture indistinct. Abdomen rather long. Legs short, spurs of foretibiae apical, three middle segments of hind tarsi short and broad.

Species composition. Monotypic genus.

Comparison. Differs from the genus *Conjunctia* in long mandibles, bluntly rounded apex of prosternal process, almost straight posterior margin of metasternum and short middle segments of hind tarsi.

Mesorabus elongatus Ponomarenko, sp. nov.
(Plate VIII, Photo 1; Figure 49a, b)

Species name coined from 'elongatus' (Latin)—elongated.

Holotype. No. 2784/1525, PIN, impression of a beetle without large part of legs. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karastau* series.

Material. Holotype.

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*So given in the Russian original. Based on earlier references to this series it should read Karabastau series—General Editor.

Description. Maximum width of body beyond shoulders. Head capsule equal in length and width, tapering in front of eyes. Genae half the length of eyes. Labrum anteriorly emarginate. Mandibles much longer than wide, apically curved. Submental lobes rather broad, notch between them shallow. Antennae scarcely extending beyond pronotal base, their first segment broad and short; second much narrower than it, almost equal in length and width; third equal to fourth and fifth together; all segments from fourth onward almost equal in length, somewhat broadening apically. Pronotum equal in length to head capsule, its lateral length two-thirds the maximum width; anterior margin of pronotum with shallow straight emargination. Propleura twice as long as wide, prosternum in front of forecoxae noticeably shorter than them. Prosternal intercoxal process much narrower than coxae, somewhat broadening beyond them, apically rounded. Forecoxae angular. Mesosternum longer than middle coxae, mesepisterna almost square, mesepimera half the length of middle coxae, almost not longer than them. 87 Length of metasternum half the width at posterior margin, anterior margin two-thirds the width at posterior, distance between coxae* 1.3 times longer than middle coxae, almost one-third the width at posterior margin of metasternum. Metepisterna slightly broadening anteriorly, posteriorly tapering strongly. Mesal processes of metepimera rather wide, extending to lateral corners of hind coxae. Hind coxae triangular, length 1.7 times the width; part of coxae projecting above abdominal plane longer than their width, posteriorly rounded, laterally emarginate. Abdomen almost two times longer than meso- and metathorax together, tapering from base of fourth visible sternite, third sternite longest, remaining sternites shorter, sutures between sternites straight. Legs short, femora uniformly thickened, length of hind femora three-times their width. Forefemora and tibiae equal in length, short, hind femora markedly longer than forefemora, shorter than tibiae, tibiae gradually broadening toward apex. Spurs of hind tibiae slightly shorter than first tarsal segment. Tibiae 1.3 times the length of hind tarsi, first tarsal segment equal to fifth or second and third together; second to fourth equal, noticeably broader than remaining segments. Integument with fine punctation, almost smooth, punctures larger only on elytral disk.

Dimensions. Body length 21 mm, width 8 mm; elytral length 12.5 mm.

Genus *Conjunctia* Ponomarenko, gen. nov.

Genus name coined from 'conjunctia' (Latin)—connection.

Type species. C. prodroma, sp. nov. Lower Cretaceous of Trans-Baikal.

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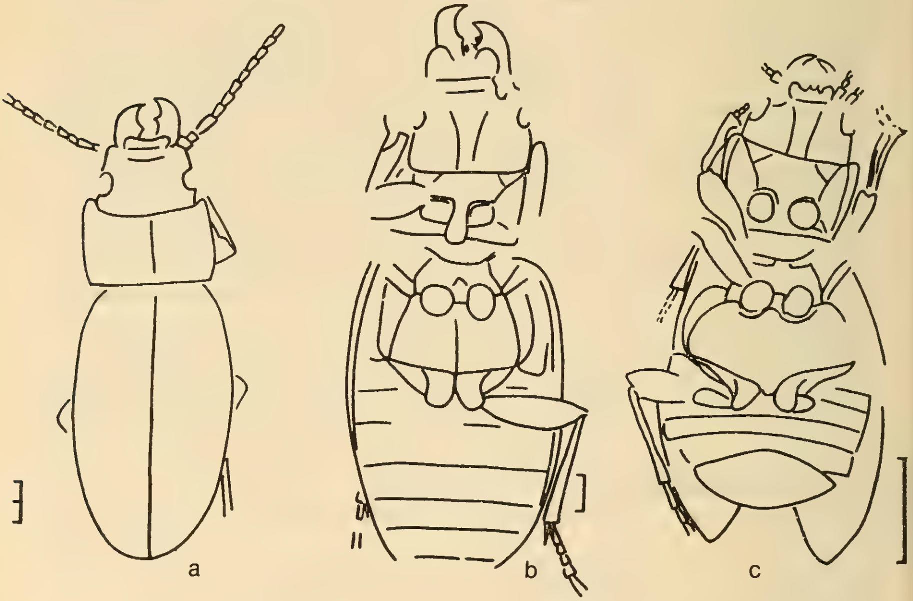
*So given in the Russian original. By context, this would imply only hind coxae, but its comparison with middle coxae raises doubt. By analogy with earlier descriptions, it is more likely that the reference is made to the distance between the middle and hind coxae—General Editor.

Description. Small, elongate, cylindrical beetle, head large, elongate, with projecting mandibles, genae much shorter than temples. Gular plate narrow. Antennae with short weakly moniliform segments. Pronotum shorter than head, transverse, weakly constricted in front of base. Propleura longer than wide. Prosternal process narrow. Mesosternum long, posteriorly angularly extending, its transverse suture indistinct. Hind coxae oblique, short, slightly separated, with weakly developed raised part. Abdomen broad and short, terminal sternites telescopic. Legs rather short, femora thickened, tibiae slightly broadening toward apex, both spurs of foretibiae apical, at same level, inner side of tibiae with groove for cleaning antennae. Segments of fore- and middle tarsi short, not broadening.

Species composition. Monotypic genus.

Comparison. Distinguished by narrow prosternal process, posteriorly angularly extending hind margin of metasternum, and a short abdomen.



86 Fig. 49. Representatives of Conjunctionini*: a, b —*Mesorabus elongatus*, sp. nov.; holotype PIN No. 2784/1525: a—dorsal view; b—ventral view; Karatau, Upper Jurassic; c—*Conjunctia prodroma* sp. nov.; holotype PIN No. 1668/1763. Baisa, Lower Cretaceous.

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*Tribe name differs from what has been given on page115—General Editor.

Conjunctia prodroma Ponomarenko, sp. nov.
(Plate VIII, Photo 2; Figure 49c)

Species name coined from 'prodroma' (Greek)—running ahead.

Holotype. No. 1668/1763, PIN, impression of an almost entire beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Beetle with flattened, posteriorly broadening body with maximum width near hind coxae. Head scarcely shorter than its width, slightly broadening beyond eyes, genae very short, eyes slightly longer than temples. Antennae attached near anterior margin of eyes. Antennal segments short, first segment twice as thick as remaining segments, second differing slightly in size from distal segments. Gular plate narrowing at middle, here its width almost half the base and one-third its maximum width. Submental lobes narrow, incision between them shallow. Pronotum two-thirds the length of head, its length almost half the width, width in front equal to head, with transverse line in front of posterior corners, anterior margin wider than 88 posterior. Propleura more than twice as long as wide, prosternum in front of coxae one-and-a-half times longer than them. Prosternal process much narrower than coxae, anterior to coxae rounded. Mesosternum one-and-a-half times longer than middle coxae, mesepisterna almost square, mesepimera short, taenioid. Distance between middle coxae and pleura not less than the width of intercoxal process. Metasternum half the width at posterior margin, width of anterior margin half of posterior; distance between hind coxae half their length. Metepisterna narrow, anteriorly sharply broadening, posteriorly proceeding as pointed narrow extension to lateral corners of hind coxae, mesal process of metepimera narrow. Width of hind coxae 3.5 times their length, raised part of coxa very slightly shorter than its width, laterally strongly emarginate. Abdomen approximately equal in length to meso- and metathorax together, five basal sternites equal in length, last sternite two-and-a-half times longer, its anterior margin projecting. Apex of abdomen blunt, rounded. All femora almost equal in length. Foretibiae equal to femora in length, slightly broadening apically, at apex with an internal process, and emarginate more proximally in apical third. Basal segment of foretarsi longer than the two following. Middle tibiae shorter than femora, scarcely broadening toward apex. Middle tarsi shorter than tibiae, first segment equal to second and third together. Hind tibiae slender, noticeably shorter than femora, basal tarsal segments long, slender. Integument with sparse, fine punctation, almost glabrous.

Dimensions. Body length 5.1 mm, width 2.1 mm; elytral length 3.1 mm.

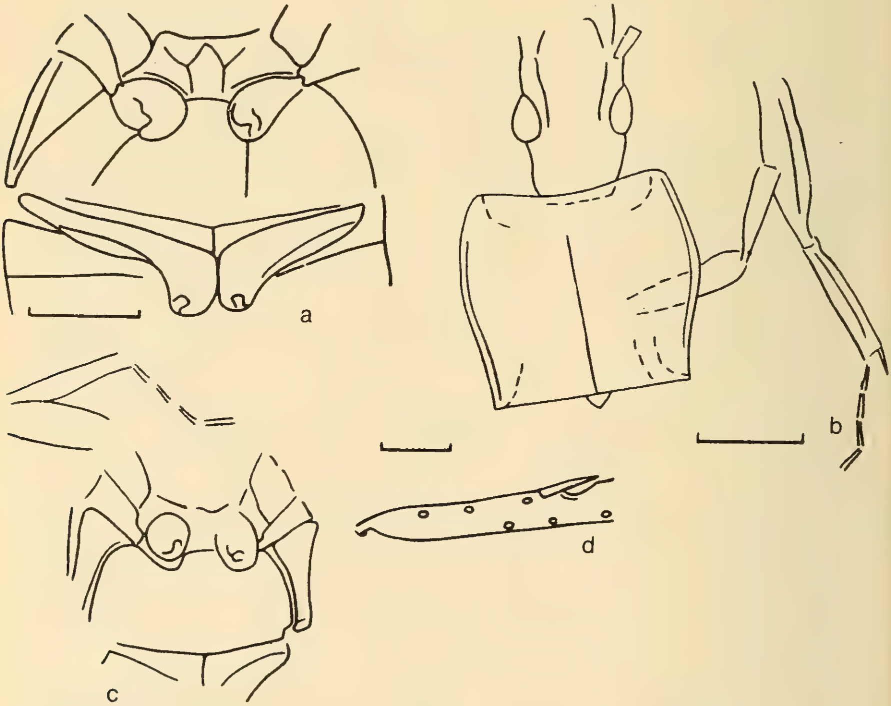
Formal genus *"Carabites"*

"Carabites" vitimensis Ponomarenko, sp. nov.
(Plate VIII, Photo 3; Figure 50a)

Holotype. No. 3064/871, PIN, impression of a beetle without head, prothorax and legs. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

89 *Description.* Small, flat, broad beetle. Mesosternum not longer than middle coxae, with depression for the apex of prosternal process. Mesepisterna almost square, only slightly short of reaching middle coxal cavities, mesepimera extending up to middle coxal cavities, rather long, laterally a



88 Fig. 50. Carabidae incertae sedis: a—*"Carabites" vitimensis,* sp. nov.; holotype PIN No. 3064/871; Baisa, Lower Cretaceous; b, c—*"Carabites" creta,* sp. nov.; holotype PIN No. 2383/111; Kzyl-Dzhar, Upper Cretaceous; d—Harpalinae, gen. sp.; specimen PIN No. 2383/206a, foretibia; Kzyl-Dzhar, Upper Cretaceous.

little longer. Anterior projection* broad, extending to anterior margins of middle coxae. Middle coxae set apart, transverse, oval. Length of metasternum approximately one-third its width at posterior margin, anterior margin half the width of posterior. Distance between [middle and hind] coxae one-and-a-half times the length [of middle coxae]. Metepisternum triangular, its inner margin almost straight, width at anterior margin half the length, posterior margin very narrow. Hind coxae triangular, contiguous, their maximum length one-third the width. Processes of femoral plates absent. Abdomen short and broad, its apex blunt, terminal sternites articulate, telescoping. Elytra with a few grooves, bearing large punctures. Integument almost smooth.

Dimensions. Body length 7 mm, width 3.5 mm; elytral length 4.3 mm.

Taxonomic position. The impression described here is the fossil remnant of a beetle, all characters of which correspond to those of the present-day carabids. However, its imperfect preservation does not allow formal comparison with the present-day forms.

"Carabites" creta Ponomarenko, sp. nov.
(Plate VIII, Photo 4; Figure 50b, c)

Holotype. No. 2383/111, PIN, isolated sclerites of a beetle, head with pronotum, meso- and metasterna, two (middle) ? legs. South Kazakhstan, Kyzyl-Ordyn oblast, Chiilii region, north-western spurs of Karatau mountain range (Kyzyl-Dzhar site). Upper Cretaceous, Turonian, Beleutin series.

Material. Holotype.

Description. Small beetle with long narrow head and long cordate pronotum. Length of head capsule slightly more than its maximum width at the level of eyes, tapering from eyes anteriorly and posteriorly. Genae shorter than eyes, temples longer than them. Sharp keel proceeding from sides of head over the eyes to the base of antennae. Basal antennal segment long and slender. Length of pronotum very slightly shorter than width, rounded anteriorly and with shallow emargination, rather strongly constricted in front of posterior angles, posterior margin straight, maximum width of pronotum anterior to middle. Meso- and metathorax together shorter than prothorax. Middle coxae set apart, mesepisterna of almost same length and breadth, mesepimera rather long, laterally broadening, extending to middle coxal cavities, middle coxae set apart**. Length of metasternum half the width at posterior margin, its anterior margin half the width at posterior, metasternal suture straight, posterior margin of metasternum angularly extending backward. Metepisternum strongly broadening anteriorly, its width posteriorly

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*Of mesepimeron—General Editor.

**An obvious repetition in the Russian original—General Editor.

three fourth the length. Metepimeron visible posteriorly between metepisternum and abdomen as a small rectangular sclerite. Legs rather short, femora only slightly extending beyond lateral body margins. Femora uniformly thickened, approximately four times longer than wide. Tibiae almost linear, most frequently flat, a little shorter than femora, with longitudinal ridge or groove, spurs of middle tibiae small. Tibiae apically with numerous small spines, large spines absent. Middle tarsi slender, equal to tibiae in length, their first segment longest, third and fourth segments shortest. Tarsal segments densely covered with small spines. Head and pronotum smooth, metasternum with large, dense tubercles.

Dimensions. Body length nearly 10 mm, length of head and pronotum 3.6 mm, length of meso- and metasterna together approximately 3 mm.

90 *Taxonomic position.* Due to imperfect preservation of the beetle it is not possible to precisely establish its taxonomic position. Nevertheless, it merits description as one of the earliest advanced carabids of the present-day type. It strongly resembles specialized present-day mollusk-eaters in the shape of its pronotum and head. Judging from the open middle coxae, exposed metepimeron, short legs and non-fossorial tibiae it must be affiliated to Isochaeta but this cannot be confirmed due to the lack of possibility of studying the apical structure of foretibiae and prosternum. Moreover, it is not definite that the small sclerite at the junction of metepisternum and hind coxa is actually the mesal part of the metepimeron.

Harpalinae, gen. sp.
(Plate VIII, Photo 5; Figure 50d)

Specimen No. 2383/206a, PIN, foretibia. South Kazakhstan, Kyzyl-Ordyn oblast, Chiilii region, north-western spurs of Karatau mountain range (Kyzyl-Dzhar site). Upper Cretaceous, Turonian, Beleutin series.

Description. Isolated foretibia of ground beetle, without apex. Small emargination in distal part of tibia, at proximal end [of emargination] large spur inserted, blocking it. Apex of spur not preserved. Two rows of large fossae for spine articulation along tibia; proximally with three grooves for cleaning antennae, and six along the opposite margin of tibia.

Taxonomic position. Judging from the nature of the groove for cleaning the antennae, the tibia belongs to a beetle of subfamily Harpalinae (sensu Crowson, 1955). This is the most ancient find of Harpalinae.

ADEPHAGA INCERTAE SEDIS

Genus *Necronectulus* Ponomarenko, gen. nov.

Genus name coined from genus *Necronectes*.

Type species. N. avus, sp. nov. Lower Jurassic of East Kazakhstan.

Description. Small, oval beetle. Head transverse, markedly longer than pronotum. Eyes rather large, longer than temples. Gular plate almost equal in length and width, somewhat narrower at middle. Antennae slender and short, extending only to base of pronotum, their segments cylindrical. Pronotum anteriorly slightly emarginate, much shorter than its width, anteriorly roundly tapering, its base not narrower than elytra at shoulders. Propleura almost equal in length and width. Prosternal process noticeably projecting beyond forecoxae. Forecoxal cavities open. Mesosternum short, with medial triangular depression for prosternal process. Mesepimera and mesepisterna almost equal. Metasternum transverse, strongly roundly tapering anteriorly. Middle coxae set apart. Metepisterna strongly broadening anteriorly, extending to midcoxal cavities. Transverse metasternal suture distinct, angularly extending backward. Hind coxae oblique, laterally completely separating metapleura and abdomen; large femoral plates present. Femoral plates transverse, laterally gradually tapered. Abdomen long, articulation of its sternites free. Elytra without grooves, with interweaving rows of large punctures.

Species composition. Monotypic genus.

Taxonomic position. Formally, judging from the metepisterna extending to middle coxal cavities and the structure of hind coxae, it must be related to subfamily Eodromeinae of the family Trachypacheidae. However, all the representatives of the latter are terrestrial whereas the fossil described here
91 is more that of an aquatic beetle. The general body shape and slender filiform antennae are indicative of this. The short propleura are also more characteristic of aquatic beetles. Unfortunately, the structure of the legs of *Necronectulus* is not known, hence it is not possible to determine its precise taxonomic position. It is noteworthy that among the present-day carabids, the representatives of Pseudomorphini morphologically resemble aquatic beetles no less than *Necronectulus* although they also lead a terrestrial mode of life.

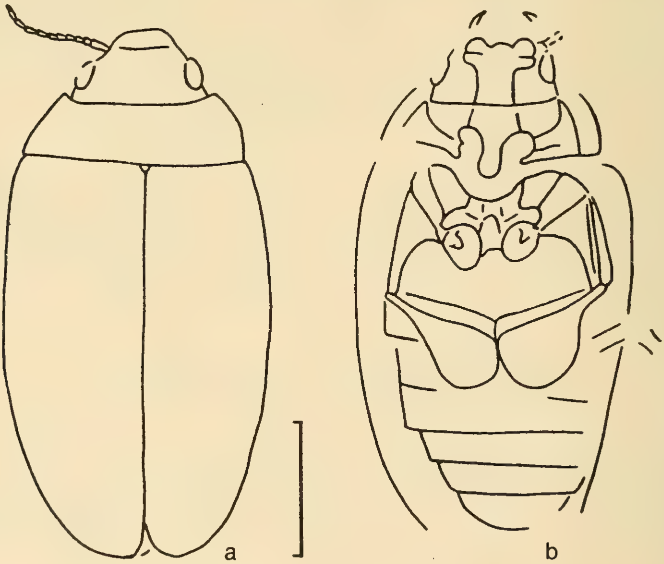
Necronectulus avus Ponomarenko, sp. nov.
(Plate VIII, Photo 6; Figure 51)

Species name coined from 'avus' (Latin)—ancestor.

Holotype. No. 1362/27, PIN, impression of a beetle without legs. East-Kazakhstan oblast, Zaisan region, Saur mountain range, right bank of Akkolka river, tributary of Karaungir (Kenderlyk site). Lower Jurassic, Tologoi series.

Material. Holotype.

Description. Length of head two-thirds its basal width, tapering in front of eyes, labrum truncate. Genae almost equal to temples in length. Mandibles rather long, acute. Lateral lobes of submentum short, rounded. First antennal segment slightly thicker than the remaining segments, equal to last two together; third segment not longer than fourth; length of flagellar segments approximately three times the width. Pronotum slightly overlapping the head, anteriorly with shallow rounded emargination. Prosternal length anterior to forecoxae and the length of coxae equal. Prosternal process slightly narrower than coxae, broadening beyond their middle, apically rounded. Propleura posteriorly very slightly broader than long, provided with pointed mesal process, partially covering forecoxal cavities. Mesosternum in front of middle coxae not shorter than them. Length of metasternum one-third the width at posterior margin, anterior margin less than half the width of posterior. Distance between middle and hind coxae one-and-a-half times greater than the length of middle coxae. Metepisterna gradually broadening in anterior half, their width anteriorly two-thirds the length. Hind coxae together with femoral plates in length two-thirds the width, reduced in lateral half, laterally short, taenioid. Abdomen tapering almost from base, last abdominal sternite at base half the width of abdominal base, its length 92 two-fifths the width. Apex of abdomen blunt. Body with fine punctation dorsally. Elytra with shallow punctures not forming regular rows. Ventral



91 Fig. 51. *Necronectulus avus*, sp. nov.; holotype PIN No. 1361/27*; a—dorsal view; b—ventral view. Kenderlyk, Lower Jurassic.

*Given as 1362/27 in the Text and Plate VIII—General Editor.

side with deeper punctures, metasternum with large punctures, fusing into transverse grooves. Thoracic pleura, femoral plates and anterior halves of abdominal sternites with smaller and sparser punctures, posterior halves of abdominal sternites with very small punctures, almost smooth.

Dimensions. Body length 4.2 mm, width 2.0 mm, elytral length 3.0 mm.

Genus Cretotaenia Ponomarenko, gen. nov.

Genus name coined from 'creta' (Latin)—chalk and 'taenia' (Greek)—band.

Type species. C. pallida, sp. nov. Lower Cretaceous. Trans-Baikal.

Description. Small, elongate aquatic larvae with ambulatory legs and rather long urogomphi. Head almost square, slightly tapering posteriorly, noticeably shorter dorsally than ventrally, hence occipital foramen shifted to dorsal side, while head was directed forward and upward during life. Parietal suture short, temporal sutures commencing almost from posterior margin of head. Ocular sclerites* large, occupying almost one-third the length of head capsule, with six large, close-set lateral ocelli. Anterior margin of head capsule without nasale, with large shallow emargination. Antennae shorter than mandibles and head capsule, their segments thick. Mandibles slender with pointed curved apices, retinaculum rather large, positioned close to the midlength of mandible. Maxillary palp four-segmented, galea two-segmented. Labium short, transverse, anteriorly projecting, without distinct ligula, its palp two-segmented. Across the head capsule there is highly sclerotized area in the form of an inverted "T"—apparently the hypopharynx.

Thoracic segments almost equal, weakly sclerotized, especially the prothorax. Mesothoracic spiracles slightly larger than abdominal spiracles, metathoracic spiracles very small, inconspicuous. Legs with rather long, cylindrical, weakly sclerotized segments.

Abdominal segments with small rounded or oval, isolated sclerotized patches, two larger on each tergite and two smaller on pleura or sternites close to spiracles. Spiracles of seven anterior abdominal segments small, that of the last segment (at posterior margin of eighth) much larger than them, converging at a distance not exceeding diameter of sclerotized patch on tergite. Ninth tergite sclerotized, pygopods short, urogomphi long, distinctly segmented.

Species composition. Monotypic genus.

Taxonomic position. Based on body segmentation, *Cretotaenia* is most closely related to carabids. However, this cannot be formally proved because of the lack of an opportunity to study the structure of the legs in detail. Moreover, aquatic metapneustic forms are absent among the larvae of carabids while the sclerotized patches on the tergites, represented by small round spots, are observed only in larvae of tiger beetles.

*See our note on page 25—General Editor.

Cretotaenia differs from all air-breathing larvae of other aquatic Adephaga by the presence of a distinct tergite on the ninth abdominal segment. Among Polyphaga, air-breathing aquatic larvae occur in Hydrophilidae but lack such long segmented urogomphi and the posterior spiracles are differently constructed. The externally similar larvae of Staphylinidae are not aquatic and lack such a large retinaculum on the mandibles. Nevertheless, this larva is most probably the larva of a beetle of the suborder Adephaga, combining the characters of both Geadephaga and Hydradephaga.

93 *Cretotaenia pallida* Ponomarenko, sp. nov.
(Plate VIII, Photos 7–9; Figure 52)

Species name coined from ‘pallida’ (Latin)—pale.

Holotype. No. 1989/2890, PIN, entire late-instar larva. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river. Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Thirty larvae from a single site, mostly entire, but due to the weak sclerotization the structural details could be examined in only a few impressions. All impressions were gathered from a single layer (Martinson, 1961).

Description. Small or minute larvae with very thin integument so that in the impressions only the following were usually visible: sclerites* of lateral ocelli, sclerotized hypopharynx, sclerotized patches on occiput and anterior margins of meso- and metathoracic tergites and round, paired sclerotized patches on abdominal segments, and main longitudinal tracheal trunks (Fig. 52a, b). Head (Fig. 52c) noticeably tapering posteriorly, dorsal length two-thirds of ventral. Coronal suture three-fourths the length of head capsule dorsally, portion of head capsule between frontal sutures triangular. Dimensions of lateral ocelli exceeding the distance between them. Sclerotized patches on parietals, sites of attachment of massator muscles clearly distinguishable on the weakly sclerotized head capsule. First antennal segment transverse, second longest, longer than third and fourth, length of third almost twice fourth. Length of mandible not less than head capsule dorsally, longer than antenna, width of mandible proximal to retinaculum one-third its length, width distal to retinaculum half of proximal, curved inward, with pointed, elongated apices. Maxilla together with palp equal in length to mandible, stipes slightly narrower than proximal part of mandible.

Prothorax noticeably shorter than head, anteriorly tapering, meso- and metathorax slightly shorter than it. Femora and tibiae of all legs approximately equal in length, tarsi somewhat shorter. Judging from the position of sclerotized patches, all abdominal segments except the ninth almost equal in length, seventh and eighth narrower than preceding segments, ninth half the

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*See note on page 25—General Editor.

length of eighth. Urogomphi 5 times longer than ninth abdominal segment. Sclerotized patches on abdominal tergites oval in late-instar larvae, elongate longitudinally, almost round in early-instar larvae. Sclerotized patches on pleurites rounded, not exceeding size of spiracle peritremes. Main longitudinal tracheal trunks thick, slightly narrower than the peritremes of the eighth abdominal segment and much wider than the peritremes of the remaining spiracles; thickness of remaining tracheae greatly exceeding them. Perimeters of spiracles highly sclerotized.

Dimensions. The larvae could be divided into two size classes. The smaller larvae differ from the larger in relatively large head, urogomphi, and sclerotized patches of cuticle. This is usually characteristic of early-instar larvae. It is therefore convenient to consider this material as composed of late- and early-instar larvae of a single species of beetle and not as belonging to different species:

Stage	Number	Length without urogomphi, mm	Width of head, mm	Diameter of sclerotised patches on tergites, mm
Late	19	av. 12.3	av. 1.0	av. 0.43
		8.0–14.3	0.8–1.1	0.4–0.5
Early	11	av. 6.1	av. 0.45	av. 0.18
		4.7–7.0	0.5–0.6	0.17–0.20

Ecology. Posterior spiracles of larvae significantly larger than remaining spiracles and shifted to postero-dorsal margin of tergite which, along with the highly sclerotized very large tracheae, indicates that these were aquatic 95 air-breathing larvae. At the same time, the same degree of sclerotization of all the peritremes, and rather large tracheal trunks extending to all the spiracles, suggests that possibly all the spiracles were functional and the larvae could live on land at least for a short time. Judging from the very weak sclerotization, the larvae could exist only in moist conditions, for example, in soil. These larvae were undoubtedly predatory. Some device for injecting digestive juices into the prey, a characteristic feature of most aquatic Adephaga, is absent in them, and during feeding they possibly held the prey above the water surface as hydrophilids do. The uplifted position of the head is also possibly associated with this since it is also characteristic of hydrophilids. No special natatory device is visible in the larvae, possibly because the weak sclerotization of the legs prevented their detailed study. However, the low level of sclerotization itself may indicate their weakness and poor locomotory activity.

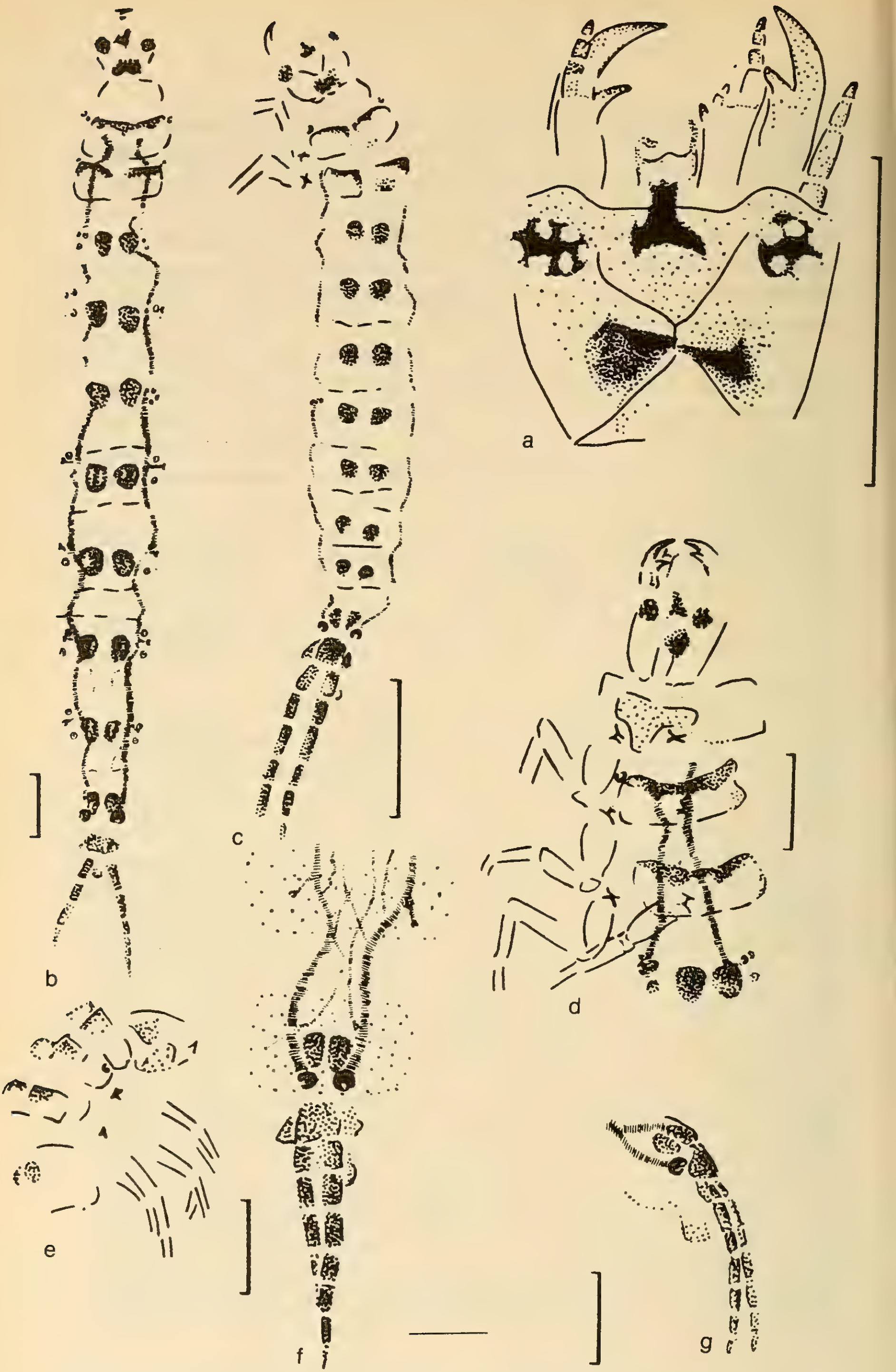


Fig. 52. *Cretotaenia pallida*, sp. nov.: a—holotype PIN No. 1989/2890, head. Paratypes: b—PIN No. 1989-2889, c—PIN No. 1989/2903, d—PIN No. 1989/2893, head and thorax, e—PIN No. 1668/1837, the same, f—PIN No. 1989/2892, tip of abdomen, g—PIN No. 1989/2900, the same. Baisa, lower Cretaceous.

Among the adult aquatic beetles found in this site, none could be definitely considered *Cretotaenia*. These were probably similar to terrestrial beetles like *Eodromeus* (family Trachypacheidae) in which many hydradephagan features are characteristically present. These beetles are very frequently found buried and most probably led a littoral mode of life.

Genus *Triadogyrus* Ponomarenko, gen. nov.

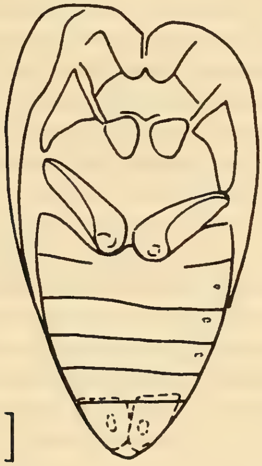
Genus name coined from Triassic, and 'gyrus' (Greek)—spin.

Type species. T. sternalis, sp. nov. Triassic of Soviet Central Asia.

Description. Mesosternum noticeably longer than middle coxae. Middle coxae equal in length and width; distance between middle and hind coxae equal to the length of middle coxae, metepisterna not extending to middle coxal cavities. Hind coxae short, without femoral plates. Abdomen with six visible sternites. Eighth sternite divided into two halves, concealed. Elytra without punctate furrows.

Species composition. Monotypic genus.

Taxonomic position. Distinctly differing from all Early-Mesozoic Adephaga in its advanced form so that formal characterization cannot completely affiliate it even to ground beetles. Also, this beetle was almost undoubtedly aquatic. This is indicated by the characteristic structure of its integument, body shape, and very large spiracles, particularly the latter. Mesosternum long, longer than practically in any other Mesozoic representative of



95 Fig. 53. *Triadogyrus sternalis*, sp. nov.; holotype PIN No. 3320/13. Garazhovka, Upper Triassic.

Adephaga, except whirligigs; structure of hind coxae resembling that of the most primitive whirligigs. This form is probably closely related to the ancestors of whirligigs.

Triadogyrus sternalis Ponomarenko, sp. nov.
(Plate III, Photo 9; Figure 53)

Species name coined from 'sternum' (Latin)—chest.

Holotype. No. 3320/13, PIN, impression of beetle without head, prothorax or legs. Ukraine SSR, Khar'kov oblast, Izyum region, mouth of Bereni river near Garazhovka settlement. Upper Triassic, Protopopov series.

96 *Material.* Holotype.

Description. Length of mesosternum half the width; mesopleura large, almost square; mesepisterna much larger than mesepimera. Length of metasternum one-third its width, posterior margin acutely angularly projecting backward. Length of hind coxae half their width. Spiracles one-fourth the length of sternites, last spiracle twice as large as preceding spiracles.

Dimensions. Body length approximately 13 mm, width 5.6 mm; elytral length 10.2 mm.

MESOZOIC STAGES IN THE EVOLUTION OF ADEPHAGA

The evolution of beetles of the suborder Adephaga differs radically from the chronoclinal changes in other suborders of beetles. Beetles of the suborder Archostemata developed as a single, rather compact group in the Permian and Mesozoic, preserving the same trends even in the relictual groups which have survived to the present. Of course, well-defined stages can be distinguished in this single process, but general morphological as well as ecological trends are preserved independently. Individual phylogenetic branches can be traced throughout the entire period of existence of the group. Therefore it is impossible to speak of temporal associations of the Archostemata as some stage in the development of this group as a whole. A similar situation is seen in the Polyphaga, with the only difference being that they evolved during the Mesozoic and Cenozoic eras. It can be said that extensive development of higher beetles (Cucujiformia) is more characteristic of the Cenozoic, whereas the less advanced forms were primarily distributed in the Mesozoic. However, all the main lineages of the Polyphaga were already widely represented in the Mesozoic, and the tendencies within these groups have been preserved without change.

The evolution of the Adephaga is totally different. Here the Mesozoic forms constitute a sufficiently unified morphological stage, although their development also proceeds along many branches. The Mesozoic fauna of the Adephaga consists almost exclusively of representatives of dead-end strictly Mesozoic branches, which became extinct toward the end of the Mesophytic (i.e., toward the middle of the Cretaceous), as did most other strictly Mesozoic groups of terrestrial animals. In the Late Cretaceous we suddenly begin to observe representatives of the essentially modern, Cenozoic fauna. Among the earliest (Triassic) Adephaga, the same forms can be observed as in the Cretaceous, though in small numbers. This certainly does not suggest that the Adephaga did not evolve in the Mesozoic. On the contrary, their evolution in individual structural features, primarily the locomotory organs, can be traced fairly well. Among the Mesozoic Adephaga, beetles such as *Coptoclava* were highly specialized for an aquatic mode of life (Ponomarenko, 1975). However, this far reaching specialization occurred in them at a primitive level of general organization.

For beetles of the suborder Adephaga, and more significantly for all Oligoneoptera, the mode of life of the larva and adult is similar, and consequently the evolutionary trends are identical for both life stages. In view of this, the Adephaga have highly prothetelic larvae. These are relatively free-living, usually active predators with fully segmented long legs, and usually compact, highly sclerotized integument. This larval type is conventionally considered to be primarily ancestral, although this assumption may be false. Unfortunately, paleontological material on the larvae of holometabolous insects is very rare, and larvae are known for only a few, primarily aquatic, species. However, this may be viewed as evidence in favor of the secondary prothetely of adephagan larvae. *Cretotaenia* is an aquatic larva with an indeterminate taxonomic position, having rather thin integument with small plate-like sclerotized patches. A similar structure is observed only in the larvae of tiger beetles. The latter constitute a group in which features of distinct specialization combine with a common, rather low level
97 of organization. It can therefore be assumed that this similarity is not accidental but reflects at least one of the modes of larval prothetely in the Adephaga. *Cretotaenia* and tiger beetles were hardly closely related and this trend is found fairly commonly in the suborder, and seen even in its distant branches.

At present, the structure of the aquatic larvae is best known among the larvae of the Mesozoic Adephaga. In fact, they are all related to the dytiscoid branch of the Hydradephaga. Larvae of the Mesozoic Gyrinidae and the Mesozoic ancestors of the Haliplidae have not yet been found. Larvae of the Mesozoic dytiscoids were already highly specialized nektonic (*Parahygrobia, Stygeonectes, Coptoclava*) or benthic (*Angaragabus*) predators with telescopic abdominal segments and with aerial respiration through the spiracles of the last abdominal segment only. Since the *Cretotaenia* too represent a distinctly aberrant off-shoot in evolution, the earlier stages of larval evolution in the Adephaga remain completely unknown. The larvae of the schizophoroid Archostemata, the direct ancestors of the Adephaga, are also unknown. Hence paleontology does not offer any new clues to the evolution of the Adephaga larvae, except for the above mentioned suggestion of a rather low level of sclerotization in the early Adephaga.

We have an incomparably large volume of material at our disposal for reconstructing the evolution of adult Adephaga, including its early stages. The origin of the Adephaga from the schizophoroid Archostemata was postulated earlier (Ponomarenko, 1969b, 1973). This assumption was based almost exclusively on the study of Archostemata and the present-day Adephaga. They study of Early Mesozoic Adephaga generally confirmed this assumption but many details differed from those postulated earlier.

Among the structural features available for paleontological study, only two characters separate the Adephaga from the Archostemata. Unfortunately, even based on these characters the suborders are not fully distinguishable even in present-day material, not to mention fossil remnants. The demarcation between the suborders is very indistinct. Both differentiating features characterize stages of consolidation of the integument for more rigid combinations of sclerites. The first feature is the character of closure of the middle coxal cavities. In all the known Archostemata the metepisterna extend to the middle coxal cavities and contribute to the closure of their lateral walls. Among the present-day Adephaga this type of structure is observed only in some diving beetles, exceptionally well adapted to an aquatic mode of life and having legs distinctly specialized for swimming, i.e., in clearly derived forms. In the lower Adephaga the metepisterna never extend to the middle coxal cavities.

Among the Archostemata for which an aquatic mode of life can be postulated, forms exceptionally well adapted for swimming are absent. On this basis, forms with an external appearance characteristic of terrestrial beetles, and with metepisterna extending to the middle coxal cavities, were described as representatives of the Archostemata (Ponomarenko, 1969b). The study of the Mesozoic Adephaga showed, however, that numerous terrestrial beetles are present among them, in which the metepisterna extend to the middle coxal cavities. Moreover, most Mesozoic terrestrial beetles had this type of structure, including those beetles in which the combination of characters categorize them as primitive ground beetles. Primitive aquatic Adephaga with a similar structure to the middle coxal cavities have also been found. This type of situation was quite expected. If the rather highly advanced Adephaga preserved the structure of middle coxal cavities characteristic of ancestral Archostemata, it would be natural to expect that a similar structure is found in more primitive extinct forms.

For the second feature—viz., the nature of articulation of the metasternum, hind coxae and abdomen—an *a priori* much higher discriminatory value may be assumed. In the Adephaga, unlike all other beetles, the hind coxae fully separate the metasternum and abdomen since they are all arranged in one plane. This condition is undoubtedly derived from the more
98 widespread one wherein the hind coxae lie above the basal, morphologically second, abdominal sternite articulating with the metasternum and fully or partially covering the basal sternite. If under these circumstances the hind coxae are strongly reduced, then the articulation of the metasternum with the abdomen, both between the coxae and along their sides, ought to proceed from the morphologically third abdominal sternite, and not the second as in the Adephaga. Several hypotheses have been advanced on the adaptive significance of the position of hind coxae characteristic of the Adephaga: adaptation for fast running, for life under bark (Crowson, 1955), and for swimming (Ponomarenko, 1973a). Functionally, however, these three trends are very similar. In each, the change is associated with the shift of the femur as far forward as possible in order to lengthen the stride of the leg in a single step.

A new difficulty arises during a study of the fossil material. It is frequently very difficult to accurately interpret the structure of abdominal base on an impression and determine whether the coxae are superimposed on the base of the abodmen or accommodated in the cavities in it. Moreover, before fossilization the body of the beetle would frequently be inflated with gases arising during putrefaction and the abdomen would be displaced from under the coxae, imitating the structure characteristic of the Adephaga. Thus the only method of understanding the interrelations of the coxae and abdomen is to carefully study the nature of the surface of the basal abdominal sternites. The parts of the abdominal sternites hidden by the coxae are almost always strongly differentiated from the other sternites by their degree of sclerotization and nature of their punctation. If we observe on the first visible abdominal sternite on each side of the coxae the same very coarse punctation that is typical of many Mesozoic beetles, we can consider that this sternite was not hidden under the coxae and that the abdominal structure is typical of the Adephaga.

Morphological studies of the abdominal base in Haliplidae are of particular significance in proving any concepts regarding its characteristic formation in the Adephaga. In these beetles, the hind coxae with their large femoral plates apparently restricted the strong forward movement of the femora. As far as we know, there are no convincing adaptive interpretations of this extravagant structure. Such a structural peculiarity has no great bearing on the hypothesis that the hind coxae developed in the Adephaga in response to life on land, since similar femoral plates could have arisen as a consequence of a transition to life in water. The meaning of this structural

feature is far more essential to the concept of an aquatic origin of the Adephaga and to the structural change in coxae as an adaptation to swimming. In many structural features the Haliplidae are the most primitive Adephaga. Their structure ought to be close to the original since a large number of Adephaga, particularly the Early Mesozoic ones, had large femoral plates, though not as large as in the Haliplidae. Femoral plates totally preclude the possibility of a forward extension of the femora, therefore the idea of inclusion of the lateral parts of hind coxae in the body wall for promoting this type of movement cannot be advanced. In fact, in the Haliplidae and Triassic Triaplidae the hind coxae are markedly different from those in the remaining Adephaga. The hind coxae of *Haliplus* are obliquely arranged and the place of attachment of the trochanter is strongly shifted posteriorly compared to the lateral part of the coxa (Fig. 54). The hind coxae in Triaplidae have a similar structure. Here neither the femoral plates nor the lateral part of the coxa obstruct the strong forward extension of the femur. Correspondingly, even the articulation of the abdomen itself strongly differs from that in other Adephaga. The second true abdominal sternite is almost entirely concealed under the hind coxae. Here its structure differs sharply from that of the other sternites. Only the small triangular areas near the postero-lateral corners have the same structure as the third sternite. A high sclerotized ridge runs along the posterior margin of this area and extends towards the body axis, closely joined to the posterior surface of the hind coxae. The ridges from both sides of the abdomen converge in the mid-line into a flat, triangular, posteriorly tapering area with sharply defined margins. This area proceeds through the third true sternite and extends into the fourth.
99 The third sternite, divided by the area into two isolated parts, seems to be identical to the second sternite of the remaining Adephaga. However, it appears that no one has considered the basic differences in the abdominal structure of the Haliplidae and the remaining Adephaga. It is noteworthy that in several other structural features the Haliplidae may be distinguished from the remaining Adephaga. The apical spiral twisting of the hind wings, which is characteristic of the Archostemata, is preserved only in them; their larvae have a unique respiratory apparatus—tracheal microgills (Seeger, 1971).

The Triassic Triaplidae which possess the largest femoral plates after the Haliplidae, apparently also resemble the latter in the structure of the abdominal base. Here also a small sclerotized area is seen in the posterolateral corners of the second true abdominal sternite; this area is structurally similar to the remaining sternites, however, the triangular area on the third sternite is absent. The medial part of the hind coxae is markedly prolonged posteriorly, the length of the coxa is comparable with its width at the anterior margin. Therefore, despite the presence of large femoral plates which are almost not at all reduced laterally, the hind femur may be advanced far forward to form not more than a 45° angle with the longitudinal axis of the body.

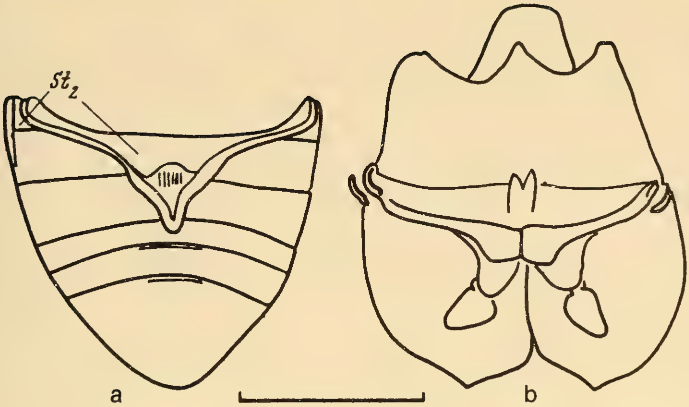


Fig. 54. *Haliplus* sp. ; a—ventral view of abdomen; b—metasternum from inside; st_2—second sternite.

The interrelationships of the Triaplidae, Haliplidae and the remaining Adephaga are presently obscure. It is unclear whether the Triaplidae may be considered the ancestors of all Adephaga in general, or whether they, together with the Haliplidae, form a sister group to the remaining Adephaga. The first assumption is supported by the very widely occurring large femoral plates among the early Adephaga. Their occurrence is apparently even more extensive than has been described. Slender femoral plates are seen usually with great difficulty in fossil remnants, and if not searched for specifically, they can be easily overlooked in all specimens, except when the abdomen is severed. Naturally this type of structure will only be included in a description when its existence is beyond doubt.

Direct evidence in support of the second assumption is lacking. There is no obvious synapomorphy between Haliplidae and Triaplidae if the large femoral plates of the hind coxae are not considered synapomorphic. These structures are unknown in the Archostemata. Such large plates are absent in other ancient Adephaga (although less developed plates are fairly common in both the Hydradephaga and Geadephaga), they are generally absent in the present-day Adephaga. It seems natural that this is a secondary character. Unfortunately, nothing can be definitely said about the functional utility of these structures. They can be viewed as a device to prevent the lowering of the legs during paddling movements in forms having a spherical coxo-trochanter articulation of the hind legs. Later on, the femoral plates become reduced with the development of the hinged articulation. However, paddling movements in all lower Adephaga, including the Haliplidae, are still highly imperfect; in fact, they do not swim but walk in water. Nevertheless, the articulation of the trochanter and coxa is already hinged in the Haliplidae.

100 Of course, we know that the Triassic Triaplidae cannot be considered the direct ancestors of all Adephaga. Quite typical Mesozoic Adephaga are observed together with them, primarily not differing even from the Late Mesozoic forms. They are represented by both terrestrial and aquatic forms, as far as can be judged from their external appearance. Apparently their separation into the Geadephaga and Hydradephaga had already taken place. Earlier a definite assumption on the origin of the Geadephaga from the Hydradephaga was expressed. However, now when the Haliplidae is clearly contrasted to both, it appears less tenable. It is not clear if the ancestor of the Geadephaga was a member of the Hydradephaga or whether both developed independently from forms closely related to the Triaplidae, while synapomorphy of the abdominal base evolved independently in them. The first theory seems preferable: the apomorphic structure of the abdominal base probably arose once in forms closely related to *Necronectulus*, and both the Geadephaga and dytiscoid Hydradephaga were derived from them. Gyrinidae appeared almost simultaneously with both. Already in the Late Triassic, there existed forms similar to *Triadogyrus*, which seem to be the direct ancestors of whirligigs. It is impossible to consider them ancestors of dytiscoids since their femoral plates are completely reduced whereas such plates are present in the lower Coptoclavidae.

At present, of all the groups of Mesozoic Adephaga we know the most about dytiscoids. Aerial respiration of larvae through the spiracles of the eighth abdominal segment is primarily a characteristic feature of this group. Already in the known ancient forms from the Jurassic there is compact segmentation of the larval abdomen. The ninth and tenth segments are reduced and the only functional spiracles of the eighth abdominal segment are positioned terminally in the middle of the posterior margin of the tergite. The rather large, bristle-bearing urogomphi were used for holding on to the surface film of water during respiration. Benthic (*Angaragabus*) and rather specialized nektonic larvae (*Parahygrobia*, *Stygeonectes*) with natatory hairs on their legs, are observed among the Jurassic dytiscoid larvae. It is noteworthy that *Angaragabus* already had suctorial mandibles with an internal canal and lacking a retinaculum, whereas the mandibles of *Parahygrobia* still had the primitive general form without a canal. This suggests that they are a prototype for the modification of mandibles of all Hydradephaga in general. The most primitive adult dytiscoids had a structure close to that of *Necronectulus*.

In the Mesozoic, dytiscoids were most widely represented by Coptoclavidae. Their remains are found in many of the Jurassic and Cretaceous sites of Asia, Europe and Africa. Judging from the eyes, which were completely separated into upper and lower, the adult beetles were pleustonic predators or scavengers. The legs were still not perfected as paddling apparatus. The most primitive Coptoclavidae (= Necronectinae), had narrow tibiae and tarsi with natatory hairs which closely resembled the legs of *Hygrobia* or *Haliplus.* Most Necronectinae still had rather large femoral plates. Their larvae (*Stygeonectes*) were active nektonic predators and in general still poorly differentiated in structure from the most primitive necktonic dytiscoid, *Parahygrobia.* However, the main characteristics of the coptoclavid larvae can already be seen in them. Their mandibles are of the cutting type, the forelegs have begun their modification into raptorial legs, and the middle and hind legs into natatory appendages.

The more advanced Charonoscaphinae are known exclusively from the Late Jurassic in which only adult beetles have been found. They clearly demonstrate considerable advancement in their adaptation toward swimming. Their body shape became more streamlined; middle and hind tibiae broadened and bore natatory hairs. The femoral plates were fully reduced; the medial part of the coxa noticeably projected above the body plane from the place of leg attachment so that the legs could move forward freely. The integument in the Charonoscaphinae was distinctly weak and through it the internal structures could be examined in detail in fossil impressions.

101 The Early Cretaceous Coptoclavinae particularly stand out in their specialization; they are as yet represented by a single species, *Coptoclava longipoda* Ping, which was nevertheless widely distributed in the Early Cretaceous of East Asia. The adult beetles were large pleustonic forms with extremely thin integument like that of the large present-day whirligigs in the genus *Dineutes*. In impressions, details of the internal structure can often be studied far more easily and conveniently than the external appearance of the beetle (Ponomarenko, 1975). The legs of *Coptoclava* resemble the legs of whirligigs. The forelegs are raptorial while the middle and hind legs are natatory with broadened segments. An oar-like surface is formed by the very broad segments of the tarsi and tibiae which lack natatory hairs. Although *Coptoclava* have the most specialized legs among the dytiscoids, they were apparently surpassed by the effectiveness of the rowing apparatus of whirligigs.

Coptoclava larvae changed less in comparison with *Stygeonectes* than did adult *Coptoclava* in comparison with *Necronectes*. Here we see essentially the same structural features but somewhat more advanced. An extra denticle developed on the mesal surface of the mandible, the raptorial forelegs and natatory middle and hind legs became more specialized, the urogomphi became longer with far more consolidated segments, and the main tracheal trunks (used as hydrostatic device) became more powerful. Overall, in *Coptoclava* both the larvae and adults are undoubtedly among the oldest and most unusual Mesozoic insects known to date.

Other dytiscoids are represented in the Mesozoic only by the [previously] discussed larvae of *Angaragabus* and *Parahygrobia* and by the adult *Liadytes*, for which a special family was suggested earlier in the text. *Liadytes* and *Angaragabus* were described as representatives of Dytiscidae in the broad sense since it was proposed that the adult and larva were possibly of one and the same species (Ponomarenko, 1963, a, b). New data neither conclusively prove nor refute this assumption but perhaps lend support to it since new structural features have been detected in the adult beetles more closely relating them to the benthic dytiscoids of Noteridae and Phreatodytidae to which *Angaragabus* is also most closely related. The Liadytidae have changed very little throughout the entire period of their documented history. Their few representatives, known from the Middle Jurassic and the end of the Early Cretaceous, could be placed in the same genus. This forms a sharp contrast with the history of the Coptoclavidae which underwent considerable morphological evolution during the same period. The Liadytidae remained slow-moving forms. Their short hind coxae and long tibiae suggest a low stroke frequency of the hind legs and slow swimming.

The remaining dytiscoid families are almost unknown from the Mesozoic. The most ancient representatives of the family Dytiscidae have been found in the Upper Cretaceous deposits of South Kazakhstan. Highly fragmentary remains have been found here almost undoubtedly belonging to a beetle combining the salient features of the most primitive tribes of the subfamilies Colymbetinae and Dytiscinae. None of the other families of dytiscoids has been found in the Mesozoic. Their absence provides further evidence against the assumption that the Hydradephaga originated from forms near Hygrobiidae or Amphizoidae. In fact, many primitive features are present in the structure of the adult beetles of these families, but the specialized structure of the larvae—with reduced terminal abdominal segments—does not permit the derivation of other Hydradephaga from them, as was done by Crowson (1955). With regard to Amphizoidae, Bell presents the valid argument (1966) that these highly advanced dytiscoids adapting to swift mountain stream lost their ability to swim. The gill breathing larvae of Hygrobiidae are more modified than the larvae of other dytiscoids. All these families, together with Noteridae and Phreatodytidae, may have originated from forms with adults similar to *Liadytes*, and larvae combining the most primitive features of *Parahygrobia* and *Angaragabus*.

The Mesozoic history of whirligigs differs significantly from that of the
102 other Adephaga and is more comparable to the evolution of the Polyphaga. The Mesozoic whirligigs do not form a single group which may be contrasted with Cenozoic whirligigs. The phylogenetic lines of extant whirligigs are clearly traceable deep into the Mesozoic, and the main evolutionary trends remain the same in the Mesozoic and Cenozoic. Of all the extant Hydradephaga, whirligigs form a unique group widely distributed in the Mesozoic; the whirligigs of the first half of the Jurassic did not differ essentially from those of the later period. At the same time, *Avitortor* are the most primitive of the known whirligigs, fragments of which were found in the Neocomian

deposits. The Mesozoic evolution of the whirligigs was very patchy. Forms with a large number of plesiomorphic features persisted for a long time and distinct evolutionary stages cannot be distinguished in their Mesozoic history. It is noteworthy that even in the Upper Cretaceous no representatives of extant families of the whirligigs have been found, although indirect indications suggest that they must have appeared right at the middle of the Cretaceous (Ponomarenko, 1973).

Different views exist on the origin and affinities of the whirligigs: from the contention that whirligigs are the most primitive of all beetles (Bradley, 1930, based on structural similarities of whirligig and sialid larvae) to the contention that the whirligigs are affiliated with the second wave of adaptive radiation of the Hydradephaga and were derived from the lower dytiscoids (Crowson, 1955, 1960). As already stated, the second contention is totally unrealistic. Of course, even the first contention is unrealistic, although it is difficult to view the similarity in the gills and anal hooks of whirligig and sialid larvae as merely the result of convergence. Undoubtedly, here we have a case, if not of direct inheritance then, at any rate, of the result of activation of similar inherited potentials. A similar structure of abdominal gills can also be seen in the diving beetle *Coptotomus* and the neuropteran *Sisyra*. In the development of these structures, the retention of embryonic abdominal legs in the larvae is obviously a result of heterochrony. Unfortunately, due to our poor understanding of the evolution of early oligoneopteran larvae this problem has not been resolved satisfactorily.

The Late Triassic *Triadogyrus*, of which we unfortunately have only a single incomplete impression, seems to be a form quite close to whirligigs. It had a rather long mesosternum; large, obliquely transverse middle coxae; hind coxae typical of primitive whirligigs, transversely triangular in shape with curvilinear forward protruding ridge separating the raised and submerged parts of the coxa; the place of articulation of the middle and hind coxae has trochanters similar to those in impressions of whirligigs. Also, the abdomen of *Triadogyrus* has six visible sternites as is usual for the Adephaga and not seven as in whirligigs in which the metepisterna extend to the middle coxal cavities. Unfortunately, the prothorax and head of *Triadogyrus* have not been preserved and hence the structure of its eyes and antennae is not known.

The aforementioned basic facts of the Mesozoic evolution of the Hydradephaga correspond best with Bell's view (1966) on the three evolutionary lines of the Hydradephaga—Haliplidae, dytiscoids, and whirligigs—and not with Crowson's view (1960) on two adaptive radiations of Hydradephaga—the earlier (Haliplidae, Amphizoidae and Hygrobiidae) and the later (Dytiscidae, Noteridae and Gyrinidae)—originating from primitive dytiscoids. However, contrary to Bell's view, these phylogenetic lines were probably not independent paths in the derivation of aquatic forms from terrestrial, but independent paths in the perfection of the aquatic mode of life already acquired by a common ancestor somewhere close to the boundary of the Permian and Triassic. The evolutionary paths followed by these three groups during the Mesozoic and Cenozoic are totally different.

The Haliplidae changed very little, hardly adapting to active swimming. In fact, the integumentary respiration of their larvae did not permit a size increase because of the more favourable volume to surface ratio possessed by smaller forms. The Haliplidae apparently were never an abundant and diverse group, and despite their relatively high population density in present-day water bodies, their feeding habits did not change during the transition
103 from the Mesophytes to the Cenophytes. Their larvae feed on Charophyta and filamentous green algae which were typical plants of the Mesozoic water bodies.

Dytiscoids were the most diverse and abundant of the Hydradephaga in the Mesozoic as well as in the Cenozoic, represented almost exclusively by extinct families; the geochronology of representatives of the then extant dytiscoid families begins only at the end of the Mesozoic (in the Late Cretaceous they were already affiliated with the Cenophytes). They may have appeared even earlier but were so rare that their remains eluded us.

Whirligigs are the only present-day family widely distributed in the Mesozoic. The number of whirligig genera known from the Mesozoic is nearly equal to that in the extant fauna. This is the first instance when an adephagan family not distinctly relictual at present, had such a wide and diverse representation in the Mesozoic. The time of origin of the extant subfamilies of whirligigs was apparently the Middle Cretaceous at the boundary between the Mesophytes and Cenophytes; however, even in the Upper Cretaceous there were still representatives of the Mesozoic groups of whirligigs. The Mesozoic whirligigs do not form a distinct taxon which could be contrasted with the Cenozoic. On the contrary, individual representatives of both eras clearly belong to the same lines which had already diverged in the Mesozoic. The Mesozoic whirligigs are distinguished not so much by structural primitiveness, as by a combination of features not present in the Cenozoic forms.

The Geadephaga undoubtedly are a more compact group than the Hydradephaga. They form a single phyletic line since the processes of morphological advancement are similar in the individual branches of the Geadephaga. Even morphologically they can be considered a fairly unified group despite the presence among them of phytophages, commensals, social insects and even parasites along with the more widespread predators. If minor adaptive modifications—at times reaching a very high level of specialization—are not considered, the basic structural plan remains the same. The Rhysodidae occupy the most isolated position. Unfortunately, the study of fossil material has not yet thrown any light on their interrelations with other beetles. The earlier view (Ponomarenko, 1968a) of their affinity with the Mesozoic forms close to the *Necromera* described by Martinson (1926) is yet to be confirmed. Therefore the Rhysodidae have been excluded from consideration in this text.

The Mesozoic Geadephaga are a fairly unified group, and distinct from the extant Geadephaga. Based on the character of the hind coxae completely separating the metasternum and abdomen, or extending to the sides only up to the lateral corners of the metasternum, they are almost since inception divided into the Trachypacheidae and Carabidae. Forms which cannot be reliably included in one family or the other are very rare, although in the Mesozoic trachypacheids the hind coxae are usually distinctly reduced laterally unlike the extant *Trachypachys.* A study of the Mesozoic Geadephaga confirms the isolation of the Trachypacheidae and their placement in a distinct separate family. However, the main evolutionary structural transformations of beetles in these two families are similar. The parallel evolution of these families led to a situation, where almost all researchers placed the present-day Trachypacheidae in Carabidae. In members of both families the femoral plates were strongly reduced and the lateral walls of the middle coxal cavities became consolidated so much so that in the extant and some Mesozoic forms, the metepisterna and then the mesepimera ceased to reach the middle coxal cavities. In many advanced forms there is a characterisitc modification in the shape of the prosternum from posteriorly broadening to narrowing before the base. Many Mesozoic ground beetles have a similar body shape and resemble the *Amphizoa* or *Metrius* in this respect. Apparently their mode of life was far less varied than in the extant carabids. However, it is rather difficult to be sure about it.

104 The Mesozoic Trachypacheidae are characterized by the inclusion of the metepisterna into the lateral walls of the middle coxal cavities and may be placed in a separate subfamily Eodromeinae. In addition, most of them have characteristically rather large femoral plates and freely articulating abdominal sternites such that the terminal ones are often telescopic. The Eodromeinae are known from the Jurassic and Early Cretaceous. The fossils of their latest representatives found in Aptian-Elbian deposits have large femoral plates and resemble the Early Jurassic forms.

In the Mesozoic, the Carabidae apparently varied widely both morphologically and ecologically. A large proportion of them belong to strictly Mesozoic taxa. They all seem to belong to Isochaeta, but in fossil remains it is difficult to determine the structure of the forecoxae that differentiates Isochaeta and Simplicia. In the subfamily Protorabinae, the metepisterna characteristically extend to the middle coxal cavities. These forms are found in the Jurassic and Neocomian. In external appearance they are very similar to the Eodromeinae and probably differed little from them ecologically.

From the Mesozoic, two markedly different, rather primitive genera of Protorabinae are known. These are *Mesorabus* from the Late Jurassic and *Conjunctia* from the Early Cretaceous. The total displacement of the pleural sclerites from the lateral walls of the middle coxal cavities is a characteristic feature of these genera. The entire coxal cavity in them is formed by the meso- and metasterna. In this diagnostic character they show parallelism with the most advanced carabid subfamily Harpalinae. They differ in external appearance from other Mesozoic ground beetles. Their body is cylindrical, elongate, with a noticeable constriction between the pronotum and elytra; externally they resemble ground beetles of the subfamily Scaritinae. Because of their closed forecoxal cavities and apical spurs of the foretibiae, they can be included only in Isochaeta or lower Simplicia. Consequently, they constitute an aberrant Mesozoic group forming an early analogue of the subsequently evolved most advanced present-day ground beetles. The more primitive subfamilies of the extant beetles such as paussinae s.l. and Carabinae were not found earlier in the Middle Cretaceous. Yet already by the Mid-Late Cretaceous, ground beetles externally strongly resembling the specialized molluskophages of the subfamily Carabinae, and even the first representative of Harpalinae are found. Thus here, as among the dytiscoids, we observe a variation in beetles in the Middle Cretaceous; the Mesozoic forms occur up to the Middle Cretaceous but subsequently the Cenozoic forms are found.

SUBORDER POLYPHAGA

Among all ancient beetles, those of the suborder Polyphaga have been studied the least. These ancient beetles are known almost exclusively from the remains of adult insects, whereas it is known that evolutionary transformations in the structure of the larvae are especially characteristic of this suborder. The main groups of this suborder are established on the basis of larval adaptations. Therefore affiliation of a beetle to many of the major groups of Polyphaga cannot be determined from the fossil adult. Beetles of this suborder often lead a cryptic mode of life and their imaginal life span is generally shorter than that of other beetles; they rarely end up in taphocenoces. The adult beetles develop frequently through regressive metamorphosis, they lose many features characteristic of adults and come to resemble pupae. Beetles of different groups resemble one another. The study of Polyphaga is rather difficult due to the diversity of this group, comprising about 150 families and several hundreds of thousands of species. This renders the classification even of the extant forms unstable and makes the study of their fossils an extremely difficult undertaking. Apparently, our information on ancient Polyphaga will remain fragmentary in the near future, and a coherent picture will not emerge. Actually, at present we study beetles which are marked by specific structures of unique external appearances which set them apart from all the diverse Mesozoic Polyphaga. Staphylinidae, Elateridae or* Rhynchophora are such types of beetles. Thus, highly specialized forms, which have ceased to evolve any further, are taken up for study while generalized forms, more interesting from the point of view of phylogeny, remain unstudied since their taxonomic position cannot be ascertained. It would be worthwhile to take a select number of these more generalized forms which are of particular interest in one respect or another, and formally describe them as a group having an unclear systematic position.

POLYPHAGA INCERTAE SEDIS

Genus *Peltosyne* Ponomarenko, gen. nov.

Genus name coined from 'pelta' (Greek)— shield, and genus *Ademosyne.*

Type species. P. triassica, sp. nov. Triassic of Soviet Central Asia.

Description. Rather large flat beetles. Head large, eyes lateral, gular plate wide. Pronotum transverse, not longer than head, anteriorly emarginate, its lateral margin sharp, pleural suture distinct. Prosternum with rather wide process slightly broadening beyond coxae, its length more than that of prothorax anterior to coxae. Forecoxal cavities posteriorly closed or almost closed by lateral projections. Forecoxae transverse, rectangular, with distinct trochanters. Mesothorax rather short, mesosternum shorter than mesopleuron, in the middle with a depression for apex of prosternal process, and with traces of transverse suture. Mesepisterna much smaller than mesepimera, remote from middle coxal cavities. Middle coxae small, set apart, with distinct trochanters. Metathorax large, metasternum slightly narrowing anteriorly, transverse metasternal suture distinct laterally, medially slightly curved backward and fusing with anterior margin of hind coxae. Metepisterna almost not broadening anteriorly, not reaching middle coxae. Metepimera somewhat broadening posteriorly, but not forming distinct mesal tonge. Hind coxae short, contiguous, posteriorly excavated but without distinct femoral plates. Abdomen with five visible sternites. Elytra with punctate grooves. Integument with dense and sharp punctation, on the elytra rugose.

Species composition. Monotypic genus.

Taxonomic position. The species described here is the most ancient of the well preserved Polyphaga known to date. It is still very similar to Ademosynidae, the representative of Archostemata very close to Polyphaga, particularly in its morphology. At that time, *Peltosyne* almost certainly already possessed a cryptopleural prothorax, and metepisterna not reaching the middle coxal cavities. It is difficult to define the position of *Peltosyne* in Polyphaga. The structure of the base of abdomen and wings is not known. Almost any attempt to combine it with any series of superfamilies (Crowson, 1955, 1971) in Polyphaga will amount to a symplesiomorphic unification. *Peltosyne* is on the whole a rather generalized type of polyphagan beetle and may be considered very close to the ancestral type of this suborder. Of course, it cannot be considered the direct ancestor of all Polyphaga. Even more rare representatives of other groups of Polyphaga, including such advanced forms as Rhynchophora, are found in the same deposits. It would not be advisable to exclude *Peltosyne* from any one of the large taxa of extant beetles or to consider it representative of a special high ranking taxon. It is more correct to describe it at present as Polyphaga incertae sedis and use the level of development of Polyphaga during the Triassic for its characterization.

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*So given in the Russian original. Since Elateridae are not a part of Rhynchophora "or" should be substituted with "and "—General Editor.

It is premature to establish to taxon of the rank of family on the basis of the genus *Peltosyne* at this stage (= Peltosynidae fam. nov.), in view of the inadequacy of the data on this form which is known from fragmentary remains.

106 *Peltosyne triassica* Ponomarenko, sp. nov.
(Plate IX, Photo 1; Figure 55)

Species name coined from Triassic.

Holotype. No. 2240/278, PIN, impression of beetle without antennae and legs. Southern Ferghana, Kirgiz SSR, Osh oblast, Batken region, Madygen area (Dzhailyaucho site). Triassic.

Material. Holotype and a fragment of elytron, specimen No. 2240/230 from the same site.

Description. Head tapering from base anteriorly, genae very short, temples about half the length of eyes. Head without distinct sutures dorsally. Mandibles rather large, fully half the length of head capsule. Gular plate broadening in anterior half. Prosternum anterior to coxae a little shorter than them. Mesosternum not longer than middle coxae, mesepisterna half the length of mesepimera. Metasternum two-and-a-half times longer than middle coxae, width of its anterior margin two-thirds the posterior. Hind coxae shorter than middle coxae. Basal four abdominal sternites equal in length, last sternite twice as long, basal width of last sternite half of abdominal base, abdomen narrowing from base of third sternite.

Dimensions. Body length 11 mm, width 6 mm, elytral length 8 mm.

Remarks. The fossils from Dzhailyaucho site underwent strong post-fossilization distortion (Ponomarenko, 1969). Hence the size of sclerites can be compared only along one of the body axes of the beetle.

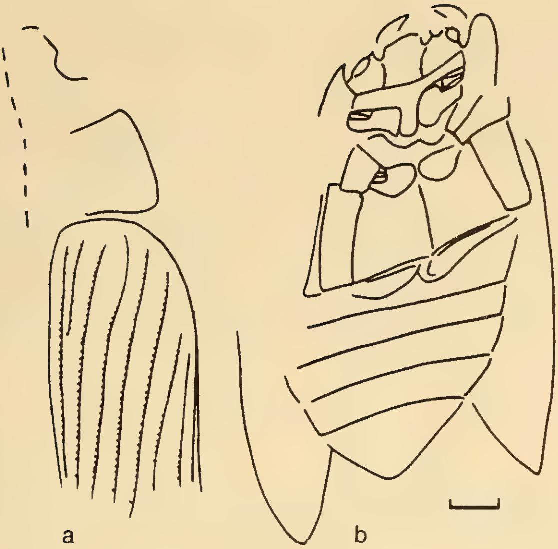

Fig. 55. *Peltosyne triassica,* sp. nov.; holotype PIN No. 2240/278: a—dorsal view; b—ventral view. Dzhailyaucho, Triassic.

INFRAORDER STAPHYLINIFORMIA LATREILLE, 1802

Family HYDRAENIDAE Mulsant, 1844

Formal genus "*Ochthebiites**"

"*Ochthebiites*" *altus* Ponomarenko, sp. nov.
(Plate IX, Photo 2; Figure 56)

Species name coined from 'altus' (Latin)—ancient.

Holotype. No. 3000/917, PIN, impression of a beetle without a large part of legs. Trans-Baikal, Buryat ASSR, Mukhorshibir region. Novospasskoe village (Novospasskoe site). Middle Jurassic, Ichetui series.

107 *Material*. Holotype and specimen No. 3000/925 from the same site.

Description. Very small beetles. Body rather wide, flat, robust. Length of head slightly shorter than average width, widest near eyes, from them narrowing anteriorly and toward base. Antennae noticeably longer than palps, their five apical segments moniliform, basal segments short. Labrum

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*Here and elsewhere in this section the genus name is incorrectly given as *Ochtebiites* in the Russian original—General Editor.

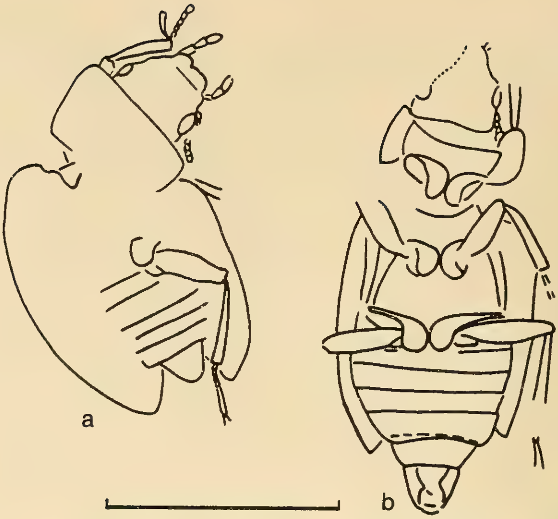

Fig. 56. "*Ochthebiites*" *altus*, sp. nov.; a—holotype PIN No. 3000/917; b—paratype PIN No. 3000/925. Novospasskoe, Jurassic.

with rather deep emargination at middle. Segments of palps short, last segment broadly lanceolate, twice as long as wide. Width at anterior margin of pronotum 1.7 times its length, narrowing beyond anterior third, posterior margin approximately two-thirds the anterior; anterior corners rounded. Prosternum noticeably shorter than forecoxae. Mesosternum almost equal in length to rounded middle coxae, latter converging. Length of metasternum two-fifths its width at posterior margin, width at anterior margin two-thirds the posterior margin, latter angularly projecting backward between coxae. Hind coxae extending backward along mid-line, overlapping almost entire first visible abdominal sternite. Abdomen with seven visible sternites, two terminal ones sharply tapering, last sternite noticeably longer than wide. Abdominal segments apparently telescoping. Legs rather short, femora weakly uniformly thickened, hind femora a little longer than middle femora. Tibiae slender, linear. Foretarsi half and hind tarsi two-thirds the length of corresponding tibiae, four* basal segments of tarsi approximately equal in length to the fourth*. No ornamentation visible on head and pronotum. Elytra with blunt grooves.

Dimensions. Body length 2.2–2.4 mm, width 1.2 mm; elytral length 1.6 mm.

Taxonomic position. Based on the structure of the distal part of antennae, palps, legs and abdomen, these fossils almost certainly belong to the family Hydraenidae whose members differ very slightly from the extant genus *Ochthebius* and closely related forms. Proximity to *Ochthebius* is seen in the short palps, and convergent middle coxae. However, these very small beetles are not sufficiently well preserved for comparison with the extant genera in which the structures of antennal base and genitalia are characteristic. These structural details are not known in the extinct forms, and since it is impossible to formally prove that they do not belong to a particular extant genus, they are placed in a formal genus, "*Ochthebiites*". The sole specific feature of the described forms is apparently the highly transverse pronotum, but this distinguishing character is hardly sufficient for establishing an independent genus. It is really remarkable that in the Middle Jurassic, forms existed which differed very slightly from the extant hydraenids.

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*Translation correct; number of segments needs verification—General Editor.

108

"*Ochthebiites*" *incertus* Ponomarenko, sp. nov.

(Figure 57)

Species name coined from 'incertus' (Latin)—uncertain.

Holotype. No. 2997/1898, PIN, impression of almost entire beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Very small beetle. Body rather wide, robust, flat. Head shorter than its width, tapering anteriorly. Length of prothorax two-thirds its width, pronotum widest in anterior third, tapering toward base and apex.

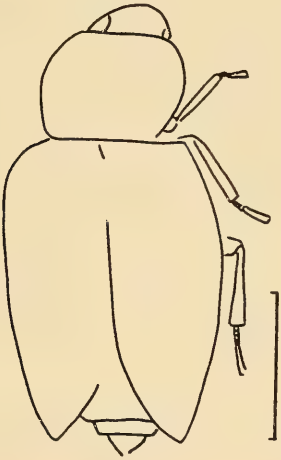

Fig. 57. "*Ochthebiites*" *incertus*, sp. nov.; holotype PIN No. 2997/1898, Karatau, Upper Jurassic.

Abdomen with seven visible sternites, last two tarsal segments slightly longer than remaining [basal] four together. Elytra with punctate grooves.

Dimensions. Body length 2.9 mm, 1.4 mm; elytral length 2.0 mm.

Taxonomic position. The beetle is extremely poorly preserved, hence its taxonomic position could not be formally confirmed. However, the structure of abdomen and tarsi suggests its inclusion in the family Hydraenidae. It is very similar to the species described above, differing only by somewhat larger dimensions, shape of prothorax and more distinct punctures on elytra.

Family HYDROPHILIDAE Leach, 1815*

Genus *Mesospercheus*** Ponomarenko, gen. nov.

Genus name coined from Mesozoic, and genus *Spercheus.*

Type species. M. tarsalis, sp. nov. Lower Cretaceous of Trans-Baikal.

Diagnosis. Small flat beetles. Head with Y-shaped suture, clypeus truncate, labrum concealed under it, palpal segments short. Pronotum transverse,
109 laterally rounded, [underside of] prothorax with grooves for antennae, and with mesal projection beyond forecoxae. Abdomen with five sternites. Last tarsal segment distinctly longer than four preceding together. Large empodium absent.

Species composition. Besides the type species, the genus includes poorly preserved remains of similar hydrophilids from the Jurassic Ichetui series of western Trans-Baikal.

Taxonomic position. Among the hydrophilids, *Mesospercheus* occupies a fairly isolated position. In the long last segments of the tarsi, it shows affinity with *Hydrochus* and *Spercheus* which are often regarded as representatives of separate monotypic families. It differs from *Hydrochus* in the absence of a freely articulating labrum and absence of transverse ridges on abdominal sternites; it more closely resembles *Spercheus* in these characters. However, specific apomorphic characters of *Spercheus,* such as the densely bristled empodium, are definitely absent in *Mesospercheus,* and the clypeus is devoid of an emargination. It has not been possible to study the structure of antennae in the available fossil material. Thus, proximity to *Spercheus* is also based on symplesiomorphy and their taxonomic unification is hardly advisable. Apparently, *Mesospercheus* is a primitive form, closely affiliated to the common ancestor of *Spercheus*, *Hydrochus*, and Hydraenidae.

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*Family Hydrophilidae is *sensu lato* considered to include *Hydrochus* and *Spercheus.*

**Given as *Mesosperchus* in the Russian original. The spelling of this genus needs to be confirmed. If it is a combination of mesozoic and *Spercheus* the correct spelling ought to be *Mesospercheus.* Compare also p. 109 of Russian original—General Editor.

Mesospercheus tarsalis Ponomarenko, sp. nov
(Plate IX, Photos 3, 4; Figure 58)

Species name coined from 'tarsus' (Latin)—sole of foot.

Holotype. No. 3015/367, PIN, impression of a beetle lacking antennae and large part of legs. Trans-Baikal, Chita oblast, Balei region, right bank of Unda river 2 km upstream from Zhidka settlement (Unda site). Lower Cretaceous, Aptian-Albian ? Balei series.

Material. Holotype and impression of an almost entire beetle, specimen No. 3063/116 from the same site.

Description. Head almost triangular, narrowing from base, its length slightly less than width. Stem of Y-shaped suture not exceeding fork in length. Clypeus large, its anterior corners rounded, middle part truncate. Gular plate narrow. Palps rather short, their apical segment longest, twice as long as wide. Pronotum short, rounded laterally, anteriorly emarginate, its length two-fifths the width. Prosternum short, much shorter than projecting forecoxae. Mesosternum shorter than middle coxae, mesepisterna slightly shorter than mesepimera, suture between them almost transverse. Middle coxae rounded, converging. Metasternal length two-fifths its width at posterior margin, width of anterior margin two-thirds the posterior. Transverse metasternal suture visible only laterally, in middle third fused with anterior margins of hind coxae. Metepisterna slightly broadening anteriorly, their width at anterior margin one-third the length. Hind coxae oblique, extending backward and broadening along midline of body. Abdomen tapering from base of second visible sternite, basal width of last sternite half of abdominal base, all five sternites subequal in length. Legs short, femora scarcely extending beyond lateral body margins. Forefemora rather strongly thickened, remaining femora slightly thickened. Tibiae uniformly broadening from base to apex and curved. Foretibiae three-fourths the length of middle tibiae, half the length of hind tibiae. Tibiae with spines laterally, foretibiae with strongly curved apical spur. Last tarsal segment one-and-a-half times longer than the equal remaining segments. Elytra with distinctly deep grooves, scutellar groove long, joining sutural groove.

Dimensions. Body length 4.0–4.1 mm, width 1.7–1.9 mm; elytral length 2.8 mm.

Comparison. Differs from the second species in shorter pronotum which is more strongly and angularly emarginate at anterior margin.

110 *Mesospercheus notatus* Ponomarenko, sp. nov.
(Plate IX, Photo 5; Figure 59)

Species name coined from 'notum' (Greek)—dorsal shield.

Holotype. No. 3000/923, PIN, impression of beetle lacking head and a large part of legs. Trans-Baikal, Buryat ASSR, Mukhorshibir region, Novospasskoe settlement (Novospasskoe site). Middle Jurassic, Ichetui series.

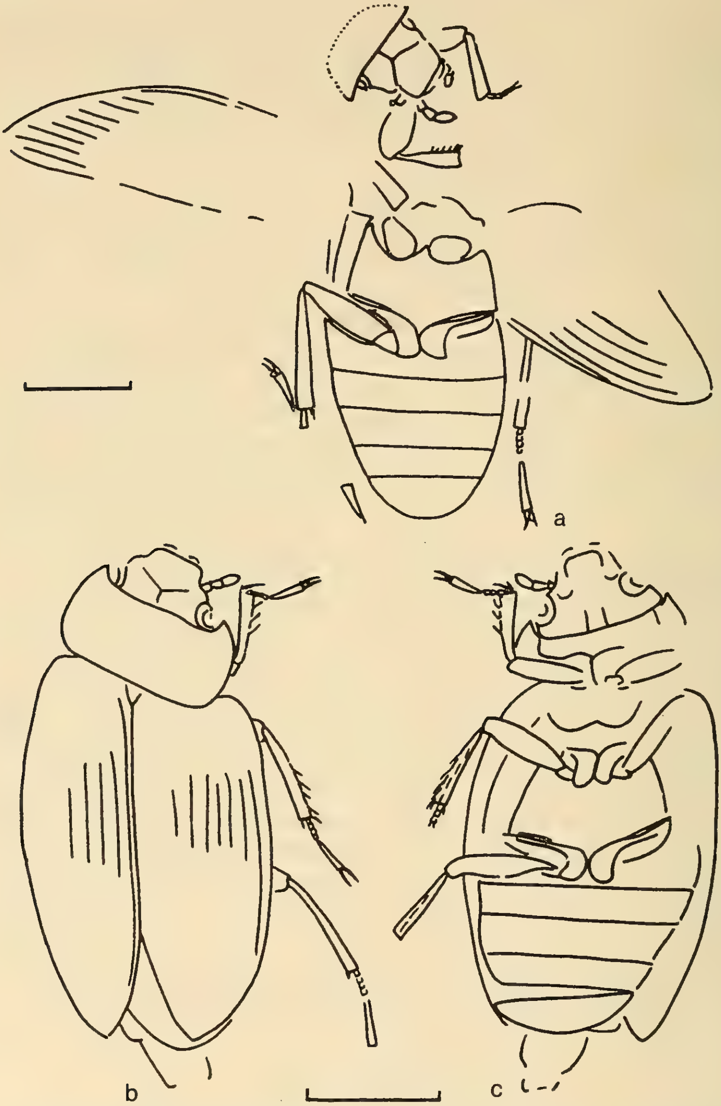


Fig. 58. *Mesospercheus tarsalis*, sp. nov.; a—holotype PIN No. 3015/367; b, c—paratype PIN No. 3063/116: b—dorsal view, c—ventral view. Unda, Lower Cretaceous.

Material. Holotype and impression of abdomen and elytra of beetle, specimen No. 3000/912 from the same site.

Description. Width of pronotum 1.8 times the length, anteriorly with shallow rounded emargination, rounded laterally, maximum width in posterior third; anterior margin markedly narrower than posterior. Underside of prothorax with distinct groove for antennae near anterior angles. Prosternum small, shorter than projecting forecoxae. Middle coxae convergent, slightly transverse, oblique. Metasternum slightly narrowing anteriorly, its length half the width at posterior margin, latter angularly projecting medially, extending between coxae. Hind coxae almost transverse, only medially extending backward. Abdominal sternites approximately equal in length. Legs short, femora scarcely extending beyond lateral body margins. Hind tibiae slightly longer than middle tibiae. Middle and hind tibiae with spines laterally. Hind tarsi half the length of tibiae, last segment one-and-a-half times longer than basal segments together. Elytra with distinct grooves, extending to outer margin apically.

111 *Dimensions.* Body length about 6.5 mm, width 2.0 mm; elytral length 5.2–5.5 mm, length of pronotum 0.8 mm.

Comparison. Differs from type species in somewhat larger dimensions, and longer, weakly anteriorly emarginate pronotum.

Remarks. Both available fossils of the beetle are fragmentary. Hence it has been affiliated to the genus *Mesospercheus* and to hydrophilids in general

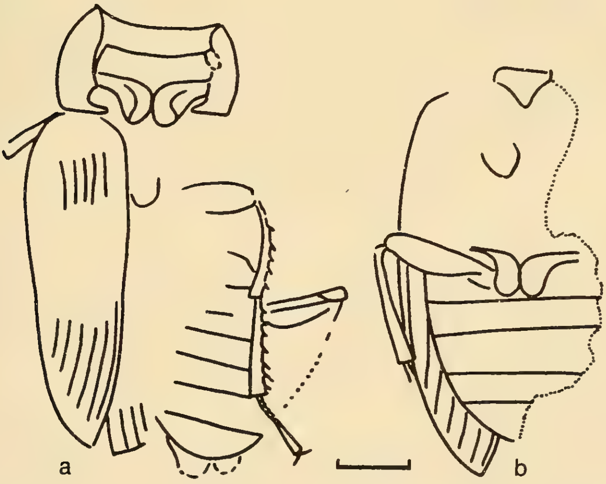


Fig. 59. *Mesospercheus notatus*, sp. nov.; a—holotype PIN No. 3000/923; b—paratype PIN No. 3000/912. Novospasskoe, Jurassic.

only on the basis of similarity with the preserved part of the body of *M. tarsalis.*

Genus *Mesydra* Ponomarenko, gen. nov.

Genus name coined from 'mesos' (Greek)—middle, and 'hydor' (Greek)—water.

Type species. M. elongata, sp. nov. Lower Cretaceous of Trans-Baikal.

Diagnosis. Small, elongate, cylindrical beetle. Head transverse, with distinct Y-shaped suture. Eyes with large ommatidia. Antennae short, with compact three-segmented oval club and monoliform short segments behind it. Pronotum transverse, with rounded sides. Elytra at shoulders scarcely wider than pronotum. Scutellum large, triangular. Wings with well-developed venation. M + Cu cell present, bending at midwing. Abdomen long, with six visible sternites, last sternite longest. Legs short, four basal segments of tarsi approximately equal to last segment or shorter. Elytra without distinct punctate grooves. Sides of pronotum and last abdominal sternite with long hairs.

Species composition. Monotypic genus.

Taxonomic position. Judging from the antennal structure and complete wing venation, this species must be included in Hydrophilidae in the broad sense considered in this work. In the structure of palps and legs it resembles ordinary Mesozoic hydrophilids. Also, *Mesydra* has several distinguishing 112 characters bringing it closer to Hydraenidae: abdomen with six visible sternites, long hairs on pronotum and abdomen, apical bend of elytra strongly shifted proximally. However, considering the possible paedomorphic nature of all these changes, it may be considered a member of Hydrophilidae whereas the Hydraenidae features developed in it independently.

Mesydra elongata Ponomarenko, sp. nov.
(Plate IX, Photo 6; Figure 60)

Species name coined from 'elongata' (Latin)—elongated.

Holotype. No. 1989/2983, PIN, reverse impression of almost entire beetle with hind wings spread. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Width of head 1.7 times its length, narrowing from base anteriorly, temples and genae very short. Y-shaped suture distinct, its stem shorter than fork, angle between fork almost 90°; fronto-clypeal suture distinct. Eyes with very large sparse ommatidia, about ten across the width of eye. Antennal club compact, its length one-and-a-half times the width.

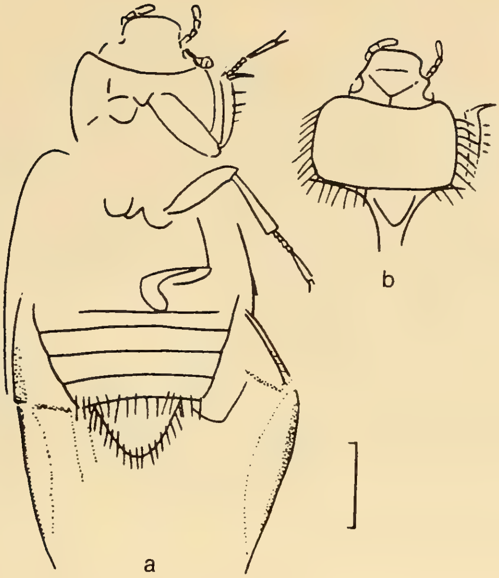


Fig. 60. *Mesydra elongata*, sp. nov.; holotype No. 1989/2983: a—ventral view; b—dorsal view of head, and pronotum. Baisa, Lower Cretaceous.

Palps not longer than head, last segment one-and-a-half times longer than penultimate. Width of pronotum 1.8 times the length, anteriorly weakly roundly emarginate, posteriorly projecting, anteriorly not narrowing, angles rounded. Scutellum as a large equilateral triangle, its sides only one-third the basal width of pronotum. Width of metasternum at posterior margin 2.5 times its length, almost not narrowing anteriorly, distance between middle and hind coxae shorter than middle coxae. Thorax and abdomen in different planes, with a noticeable drop in elevation between. Abdomen tapering from base of third visible sternite, basal width of fifth sternite two-thirds of abdominal base, width of the sixth sternite half the abdominal base. Length of last sternite half its basal width, almost twice as long as remaining sternites. Forefemora slightly but uniformly thickened, nearly equal in length, tibiae slightly shorter than them, slightly broadening from base to apex. Foretibia with large curved spur. Foretarsi slightly shorter than tibiae, last segment almost one-and-a-half times longer than preceding segments together. Middle tarsi two-thirds the tibiae, last segment equal to penultimate. Wings 113 approximately twice as long as elytra. Body with fine indistinct punctation.

Dimensions. Body length 5.6 mm, width 2.3 mm; elytral length 3.3 mm, wing span 5.8 mm.

Genus *Mesohelophorus* Ponomarenko, gen. nov.

Genus name coined from Mesozoic, and genus *Helophorus.*

Type species. M. sibiricus, sp. nov. Lower Cretaceous of Trans-Baikal.

Diagnosis. Small, flat beetle. Head large, with distinct Y-shaped suture on top. Pronotum strongly transverse, trapezoidal, weakly narrowing anteriorly, laterally flat, disk with longitudinal grooves. Middle coxae convergent, with keel-shaped intercoxal process. Abdomen with five visible sternites. Legs short, last segments of fore- and middle tarsi equal to all the preceding segments [together], last segments of hind tarsi shorter than them. Elytra with sharp punctate grooves.

Species composition. Monotypic genus.

Taxonomic position. This genus exhibits a distinct similarity with *Helophorus* in the characteristics of tarsi, transverse not anteriorly narrowing pronotum and the structure of middle coxae. In the laterally flat-sided pronotum with distinct corners, this genus generally differs from all hydrophilids including *Helophorus*, it also differs in the structure of elytra. *Mesohelophorus* has only three longitudinal grooves on the disk of the pronotum, and not five as in *Helophorus.*

Mesohelophorus sibiricus Ponomarenko, sp. nov.
(Plate IX, Photo 7; Figure 61)

Species named after Siberia.

Holotype. No. 3063/841, impression of beetle lacking antennae and large part of legs. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype, incomplete beetle no. 3064/931 isolated elytron No. 1989/2998 from the same site.

Description. Length of head a little less than width, widest near eyes, tapering toward base, triangular in front of eyes. Eyes convex. Stem of Y-shaped suture slightly shorter than fork, angle between fork obtuse. Gular plate narrow. Antennae difficult to see, apparently of structure normal for hydrophilids, with two long basal segments followed by three short, moniliform segments; club oval, three-segmented, wide capsular, thick and compact. Antennae slightly extending beyond prothorax. Length of pronotum almost one-third the width at posterior margin, anterior margin scarcely narrower than posterior, pronotal angles almost right-angled. Anterior margin weakly roundly emarginate, posterior slightly projecting. Middle part of pronotum approximately half its width, [taking the form of a] raised flat dome above the flattened lateral fourths. Longitudinal groove passing medially through the dome, deepening into a pit at posterior margin of pronotum. Shallower grooves running on both sides of the dome. Sides of pronotum margined with narrow lines. Mesosternum scarcely shorter than middle coxae, mesepimera oblique, their length less than width. Middle coxae rounded, triangular, closely convergent; long, narrow keel-shaped mesosternal projection and short broad metasternal process present between them.

114 Length of metasternum two-fifths the width at posterior margin, width at anterior margin two-thirds that at posterior. Metepisterna strongly broadening anteriorly, hind coxae transverse, length of its raised part reduced laterally, elongate posteriorly along the mid-line; lateral margin of elongate medial part emarginate. Abdomen short, not longer than meso- and metathorax together, narrowing posteriorly from base of last sternite, width of the latter half of abdominal base. All sternites almost equal in length, freely articulate. Apices of slightly thickened femora scarcely extending beyond lateral body margins. Fore- and middle tibiae noticeably shorter than femora, hind tibiae equal to them. Foretarsi approximately half the length of tibiae, middle tarsi equal to tibiae, hind tarsi slightly longer. Last segment of hind tarsus equal to the two preceding. Elytral grooves running parallel to sutural margin. Scutellar groove long, not shorter than one-third of elytron. Intervals between punctures in furrows only a little larger than the punctures themselves. Integument strongly punctate. Sinciput, occiput and pronotum with large, coarse punctation, intervals between punctures not larger than punctures themselves, elytra and large part of body ventrally shagreened, underside of pro- and mesothorax with rather fine dense punctation.

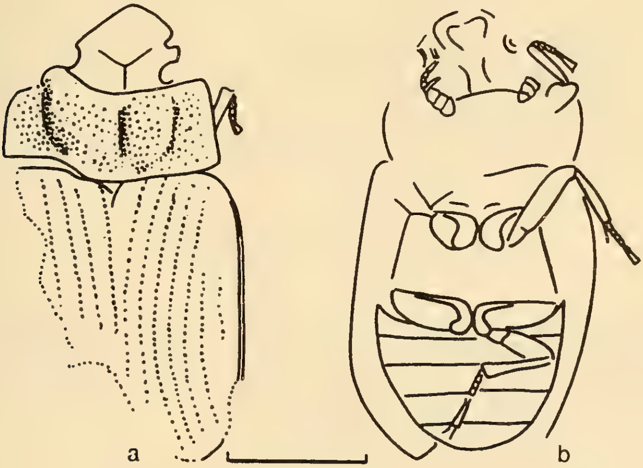


Fig. 61. *Mesohelophorus sibiricus*, sp. nov.; holotype PIN No. 3064/841: a—dorsal view; b—ventral view. Baisa, Lower Cretaceous.

Dimensions. Body length 3.5 mm, width 1.8 mm, elytral length 2.1 mm.

Genus *Paraspercheus* Ponomarenko, gen. nov.

Genus name coined from genus *Spercheus.*

Type species. P. asiaticus, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Rather large, flat, broad-beetles. Head large, elongate, partially covered by pronotum. Y-shaped suture indistinct. Antennae rather long, with long, slender basal segments and compact, oval, three-segmented club. Pronotum transverse, rather strongly narrowing anteriorly, anteriorly emarginate. Forecoxae large, projecting. Mesosternum slightly shorter than middle coxae. Middle coxae large, slightly separated, almost equal in length and width, with prominent anterodorsal part. Metasternum strongly transverse. Hind coxae contiguous. Abdomen with five sternites. Foretibiae with large curved spur. Last segment of tarsi longer than preceding ones together. Large empodium absent. Elytra without grooves. Integument with coarse punctation.

Species composition. One species from Late Jurassic of South Kazakhstan and one species from Early Cretaceous of Trans-Baikal.

Taxonomic position. Genus *Paraspercheus* occupies the most isolated position among Hydrophilidae s. l., i.e. hydrophilids having a normal abdomen with five visible sternites. Trailing legs with a very long last segment are observed in only a few small, distinctly relictual forms. In general, 115 *Paraspercheus* is related to the largest hydrophilid beetles. It differs markedly from other hydrophilids in possessing very coarse punctation of the integument, totally lacking traces of grooves on the elytra and also in the absence of a large empodium; the latter structure is highly characteristic of many hydrophilids, at least of forms with an enlarged middle tarsal segment. The empodium is definitely absent in *Paraspercheus* since if it could be seen in fossils of small hydrophilids then it ought to be seen in the well preserved tarsi of *Paraspercheus vitimensis.* Apparently *Paraspercheus* is a representative of the special Mesozoic line of hydrophilids.

Paraspercheus asiaticus Ponomarenko, sp. nov.

(Plate IX, Photo 8; Figure 62)

Holotype. No. 2997/552 [*sic*], PIN, impression of almost entire beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of the Kashkarata river valley, Aulie area in Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype and impression of one almost entire beetle, specimen No. 2239/1224 from the same site.

Description. Head slightly longer than wide, slightly narrowing anteriorly, with constriction in front of base, length of temples half the eyes, genae

almost equal to eyes in length. Y-shaped suture weak, its stem longer than fork, angle between fork obtuse. Gular plate narrow. Clypeus and labrum strongly projecting anteriorly, labrum long, distinct, degree of its sclerotization distinctly second to that of clypeus. Mandibles rather long, strongly projecting anteriorly. Three basal antennal segments equal in length, first noticeably thicker than second and third, following segments shorter than third in length, slightly moniliform; three apical segments forming rather compact oval, asymmetric club. Length of pronotum half its width, laterally rounded, narrowing anteriorly and posteriorly, widest at middle. Prosternum shorter than large projecting forecoxae. Distance between middle coxae approximately one-third their width. Mesepimera transverse, short. Width of metasternum at posterior margin 3.5 times its length, width at anterior margin
116 two-thirds of posterior. Distance between middle and hind coxae less than the length of middle coxae. Metepisterna slightly broadening anteriorly. Hind coxae transverse, their raised medial parts extending backward and laterally. Abdomen longer than meso- and metathorax together, tapering from base of third sternite; basal four sternites equal in length; last segment one-third longer, triangular, its basal width half of abdominal base. Legs noticeably extending beyond lateral body margins. Forefemora almost equal to middle femora and two-thirds the hind femora. Foretibia slightly shorter than femora,

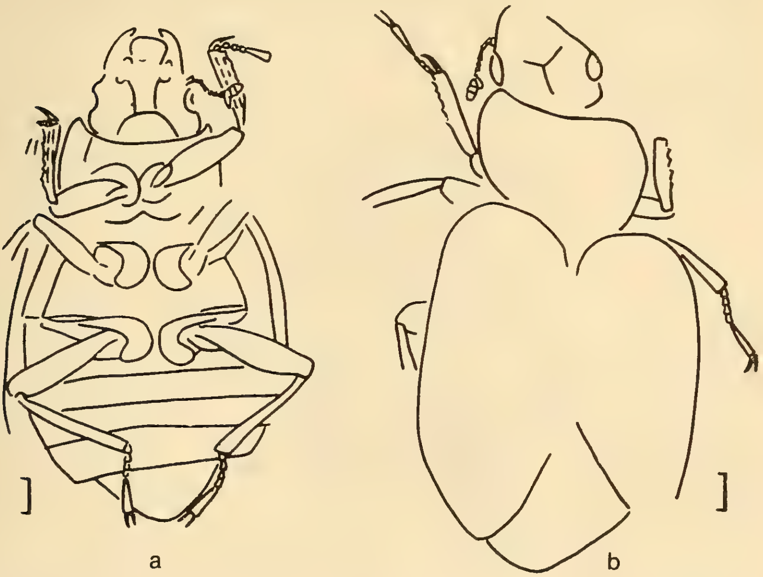


Fig. 62. *Paraspercheus asiaticus*, sp. nov.; a—holotype PIN No. 2997/522, b—paratype PIN No. 2239/1224. Karatau, Upper Jurassic.

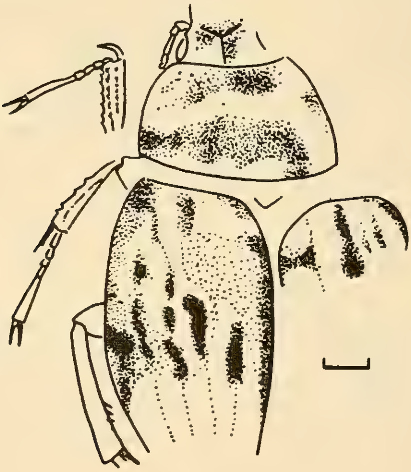
flat, with grooves and rows of spines laterally. Apical spur of foretibiae reaching third tarsal segment. Middle tibiae noticeably shorter than corresponding femora, narrower than foretibiae. Hind tibiae slender, linear, 1.4 times longer than foretibiae. Foretarsi only slightly shorter than foretibiae, first segment much shorter than second, last noticeably longer than the remaining segments together. Middle tarsi not shorter than tibiae, their last segment scarcely longer than remaining segments together. Hind tarsi approximately half the hind tibiae, last segment slightly longer than remaining segments taken together. Claws large, weakly curved. Sinciput, occiput, pronotum and prosternum with coarse punctation, punctures on meso- and metasterna smaller and dense, elytra with large scattered punctures.

Dimensions. Body length 14–15 mm, width 8 mm; elytral length 9 mm.

Comparison. Distinguished by pronotum narrowing toward base, longer head, narrow foretibiae, and absence of distinct ornamentation.

Paraspercheus vitimensis Ponomarenko, sp. nov.
(Plate IX, Photo 9; Figure 63)

Holotype. No. 3064/1071, PIN, incomplete reverse impression of beetle, only structure of dorsal side and part of legs visible. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.



117 Fig. 63. *Paraspercheus vitimensis*, sp. nov.; holotype PIN No. 3064/1071. Baisa, Lower Cretaceous.

Material. Holotype.

Description. Oval beetle. Head rather strongly retracted under pronotum, noticeably longer than wide, weakly tapering anteriorly. Y-shaped suture weak, its stem much longer than fork, angle between fork obtuse, mandibles strongly projecting anteriorly. First to third segments of antennae long; 4th shorter than them, transverse. Width of pronotum at posterior margin 1.8 time its length, roundly tapering anteriorly, width at anterior margin two-thirds the posterior. Foretibiae scarcely shorter than middle tibiae, two-thirds the hind tibiae, broad and flattened, with longitudinal groove and two rows of spines; spines of outer row larger and sparser than inner row. Tibiae with denticles laterally. Spur of foretibiae strongly curved, equal in length to three basal segments of foretarsi. Middle tibia broadening from base to apex, with longitudinal groove, laterally serrate, spur of middle tibiae shorter than two basal tarsal segments. Foretarsi equal to tibiae in length, first segment shorter than second, last noticeably longer than all preceding ones together. Middle tarsi equal to middle tibiae, their three basal segments equal, slightly shorter than fourth segment, together with it equal
117 to fifth. Claws long, almost straight. Dorsal body surface with coarse punctures, somewhat finer punctures on head. Intervals between punctures smaller than punctures themselves. Pronotum with dark, transversely oval spot in front of posterior margin, elytra with dark colored suture and four longitudinal dark colored bands on the disk laterally.

Dimensions. Body length about 13 mm, width 7.5 mm; elytral length 8.5 mm.

Comparison. Differs from the type species in the more retracted head, pronotum narrowing from base, and broad forefemora. Probably merits status of an independent genus.

Family SILPHIDAE Latreille, 1807

Genus *Mesagyrtes* Ponomarenko, gen. nov.

Genus name coined from Mesozoic and genus *Agyrtes.*

Type species. Mesagyrtes communis, sp. nov.; Jurassic of Trans-Baikal.

Description. Small elongate-oval beetle with short slender legs. Head equal in length and width, widest at occiput, whence narrowing anteriorly. Eyes slightly protuberant, ocelli present on hind corners of sinciput. Antennae extending beyond pronotal base, their distal segments broadening, forming loose club. Segments of maxillary palps cylindrical, last segment only slightly larger than penultimate, not dilated. Pronotum transverse, narrowing from middle anteriorly far more strongly than posteriorly, scarcely narrower than elytra at shoulders, flat lateral margin absent. Scutellum rather large, triangular. Prosternum short, distinctly emarginate anteriorly, taenioid, much shorter than forecoxae. Forecoxae projecting, but rather short, with long narrow lateral process. Foretrochanters virgate. Mesosternum shorter than middle coxae, mesepimera equal to middle coxae in length. Metasternum transverse, with distinct transverse and longitudinal metasternal sutures. Middle coxae slightly transverse, oblique, projecting. Metepisterna not broadening anteriorly. Hind coxae contiguous, transverse, short. Abdomen with five visible sternites, last sternite not longer than preceding ones, apically truncate. Elytra with very blunt longitudinal grooves beset with faint punctures. Femoral apices scarcely extending beyond lateral body margins, femora slightly and uniformly thickened, tibiae slender, slightly broadening toward apex, tarsi with slender cylindrical segments.

Species composition. Monotypic genus.

Taxonomic position. Based on elytra with punctate grooves, the genus stands closest to tribes Agyrtini and Pterolomini, however, the grooves are much weaker than in the representatives of these tribes. The presence of ocelli most closely relates it to Pterolomini though the abdomen with five sternites puts it closest to Agyrtini. The shape of its body places it intermediate between these tribes. With only one specimen of this rather isolated form, it is difficult to define its exact place in the family.

Mesagyrtes communis Ponomarenko, sp. nov.
(Plate X, Photos 1–3; Figure 64)

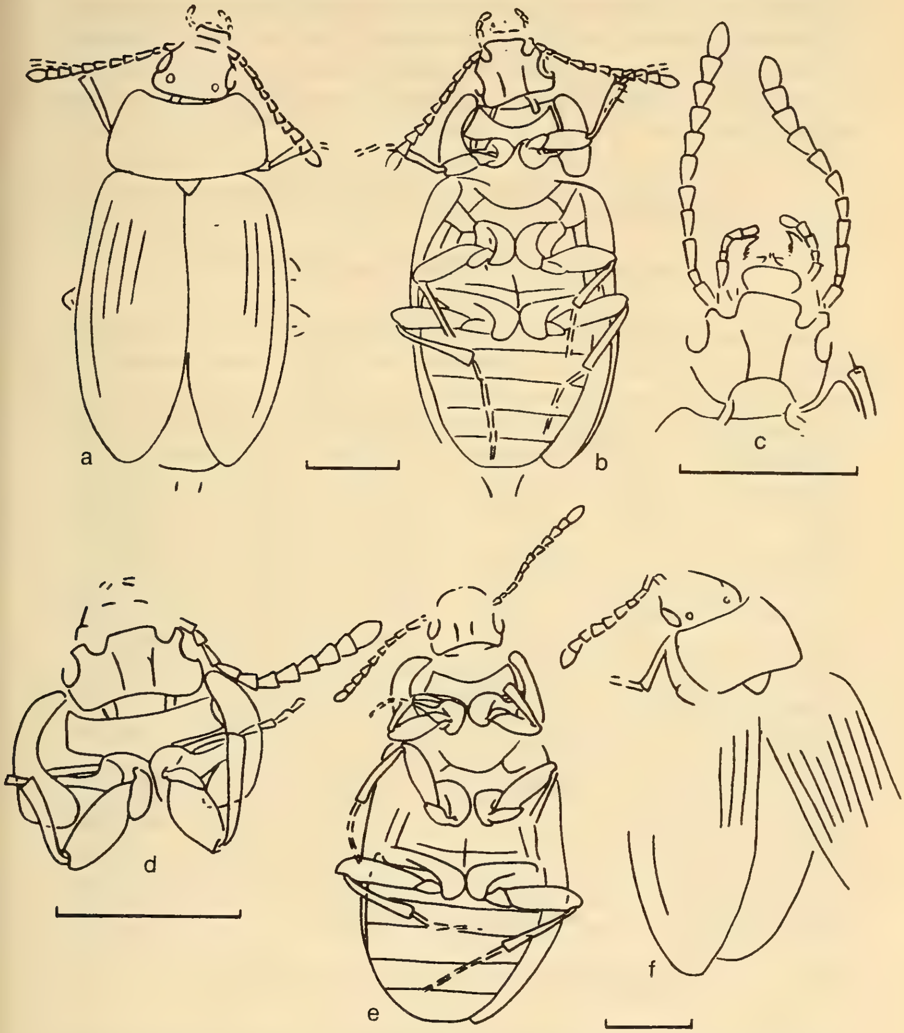
Species name coined from 'communis' (Latin)—common.

Holotype. No. 3000/926, PIN, impression of almost entire beetle. Trans-Baikal, Buryat ASSR, Mukhorshibir region, north of Novospasskoe settlement (Novospasskoe site). Middle Jurassic, Ichetui series.

118 *Material.* Besides holotype, 6 impressions of almost entire beetles, specimen Nos. 3000/909, 910, 913, 916, 920, 929, impression of head and pronotum, specimen No. 3000/915 from the same site, reverse impression of entire beetle, No. 2744/12 from Novaya Bryan' site, Buryat ASSR, Mukhorshibir region, Bryanka river, Ichetui series.

Description. Length of head capsule two-thirds its width, temples shorter than eyes, genae short. Gular plate longer than wide. Labrum slightly emarginate apically. Last segment of maxillary palps 1.5 times longer and slightly thicker than penultimate. First antennal segment noticeably thicker and longer than second; second half the length of third; third thinnest of all, almost not broadening towards apex, slightly longer than fourth; fourth and fifth noticeably broadening toward apex; fifth two-thirds the third; fifth to tenth segments equal in length, strongly broadening toward apices; apex of ninth twice as wide as apex of fourth; last segment ovoid, equal in length to third. Length of pronotum approximately half its width, roundly emarginate at anterior margin, rounded laterally, width of its posterior margin 1.7 times
119 the width at middle. Length of prosternum one-fifth its width. Lateral process

of forecoxae not narrower than coxae themselves. Mesosternum half the length of middle coxae. Width of mesepisterna approximately half of mesepimera. Middle coxae with sharply truncate and flat lateral part. Length of metasternum half its width; when middle coxae extending backward, then



118 Fig. 64. *Mesagyrtes communis*, sp. nov.: a, b—holotype PIN No. 3000/926: a—dorsal view, b—ventral view. Paratypes: c—PIN No. 3000/915, d—PIN No. 3000/913, e—PIN No. 3000/909, all from Novospasskoe, Jurassic; f—paratype PIN No. 2744/12, head; Novaya Bryan', Jurassic.

distance between middle and hind coxae less than length of middle coxae. Length of hind coxae half their width, rather sharply reduced beyond mesal third. Abdomen tapering from second visible sternite, basal width of last sternite half of abdominal base, first visible sternite one-and-a-half times longer than second, remaining sternites almost equal. Length of forefemora two-thirds the middle femora, half of hind femora, all tibiae slightly shorter than femora, apices of foretibiae not extending. Tarsi with slender, virgate segments, slightly less than tibiae in length.

Dimensions. Body length 4.6–5.2 mm, width 1.8–2.3 mm; elytral length 2.7–3.0 mm.

INFRAORDER SCARABAEIFORMIA

Family SCARABAEIDAE Latreille, 1802

To date, available information on Mesozoic Scarabaeidae was primarily confined to the single Early Cretaceous *Proteroscarabeus* Grabau. The actual affiliation of the remaining forms mentioned here remained absolutely debatable. It must be noted that one of the presumed scarabaeids-*jurassicus* Oppenheim, 1888, was generally described from the impression of a cockroach and not a beetle (Ponomarenko, 1971). In the Lower Cretaceous deposits of Trans-Baikal numerous remains were found whose sublineal affiliation within the family Scarabaeidae is certain. Almost all the remains are well preserved intact specimens, and even the structure of hind wings and position of abdominal spiracles can be successfully studied in some of them. However, it is a difficult task to establish the precise taxonomic position of the described forms. The formal affiliation of scarabaeids to a subfamily requires knowledge of the structure of antennae and position of abdominal spiracles. These distinguishing characters usually cannot be sufficiently well studied in fossil remains. The use of indirect, often habitual characters for such ancient forms is risky. Their comparison with Cenozoic forms therefore becomes impossible and even the described genera should be considered formal. The family Scarabaeidae is considered here *sensu lato* to include Geotrupidae. The described forms apparently belong strictly to Scarabaeidae, but it is not always possible to substantiate it.

Genus *Geotrupoides* Handlirsch, 1906-1908

Type species. Geotrupes lithographicus Deichmüller, 1886. Upper Jurassic of western Europe.

Diagnosis. Rather broad, flat beetles. Head transverse, mandibles and labrum clearly visible from under the clypeus. Pronotum transverse, laterally rounded, rather long. Elytra with distinct punctate grooves.

Species composition. One species in the Late Jurassic of western Europe, two in the Early Cretaceous of Trans-Baikal.

Taxonomic position. The relations between *Geotrupoides* and other Scarabaeidae remain unclear. Its position remains ambiguous even after the study of new material which is far better preserved than the single specimen of the type species. The genus is considered by us as formal since species in a natural genus cannot differ so markedly as the newly described species do from the type species. Labrum and mandibles of *Geotrupoides* project far out 120 from under the clypeus. Among Pleurosticti, only Glaphyrinae have a freely articulate labrum but they lack distinctly punctate elytral grooves. Among Laparosticti, *Geotrupoides* most closely resembles representatives of small primitive families closely related to Hybosorinae, but an extensive comparison is not possible since the structure of antennae and abdominal spiracles could not be studied in any of the specimens.

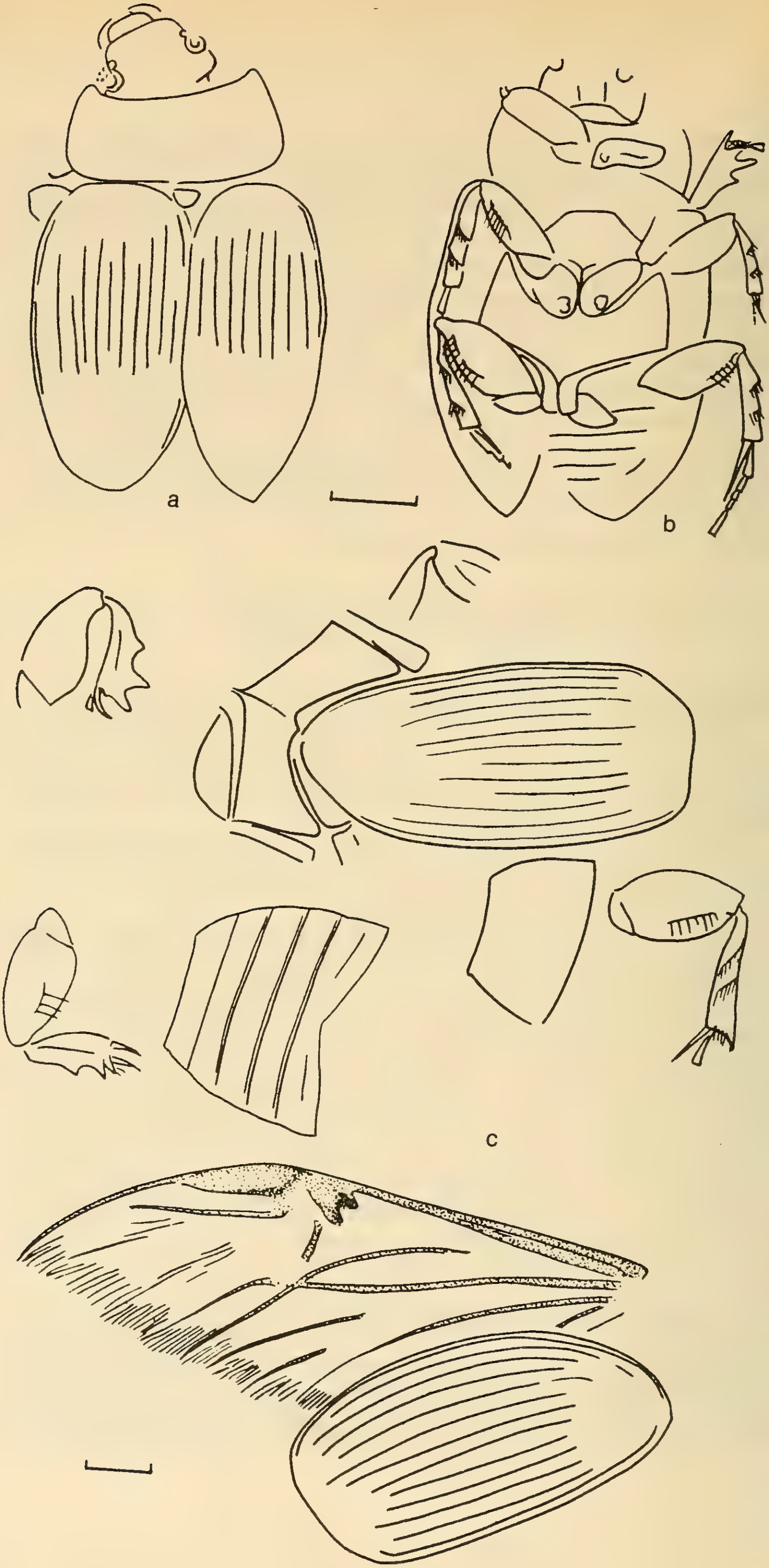
Geotrupoides sulcatus Nikritin, sp. nov.
(Plate X, Photos 4, 5; Figure 65)

Species name coined from 'sulcatus' (Latin)—grooved.

Holotype. No. 1668/1785, PIN, almost entire impression of beetle, Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Besides holotype, three impressions of almost entire beetles from the same site, specimen Nos. 1668/1801, 1989/2970, 3064/867, one of which is dismembered into individual sclerites.

Description. Body broadly oval. Head almost equal in length and width, widest at eyes and at temples, with small emarginations in front of eyes, clypeus broad, rounded laterally, anteriorly truncate. Labrum rather long, anteriorly blunt. Mandibles apically with well-developed denticles, considerably projecting from under the clypeus. Pronotum transverse, its length less than half its width, almost not narrowing anteriorly, laterally somewhat rounded. Prosternum very short, much shorter than highly transverse forecoxae. Width of forecoxae 2.5 times the length, with distinct keel. Mesosternum long, with distinct posterior extension. Mesopleura large, mesepisterna and mesepimera approximately equal in length, pleural sutures almost anteriorly directed. Middle coxae oblique, strongly transverse. Scutellum semicircular. Width of metasternum 2.5 times its length, almost not anteriorly narrowing, metepisterna very slightly broadening anteriorly. Posterior margin of metasternum angularly projecting backward. Hind coxae large, slightly broadening laterally, its raised part running along metasternum as a narrow band, extending backward along midline. Abdomen tapering from base, sternites almost equal in length, freely articulating and may be


a
b
c

121 telescoped one under the other. Legs short, femora not extending beyond lateral body margins. Femora broadened, forefemora 2.5 times and others 2 times longer than wide. Middle and hind femora each bearing two rows of long hairs. Tibiae slightly shorter than femora, hind tibiae longer than middle and foretibiae. Foretibiae flat and broad, with three denticles on outer margin in anterior half, middle denticle noticeably larger than the remaining. Middle tibiae not broad, with two transverse keels bearing stiff hairs. Spurs of middle tibiae equal to two basal tarsal segments in length. Hind tibiae broadening, its apical width one-third its length, with two transverse keels weaker than those of middle tibiae. Keels and apices of tibiae with rows of stiff bristles. Spur of hind tibiae long, equal in length to three basal tarsal segments. Foretarsi small, half as long as tibiae, basal segment equal to the following two together, second to fourth segments equal in length, last equal to the three preceding. Middle and hind tarsi scarcely shorter than tibiae, their basal segments equal to the two following, last segment slightly shorter than first. Elytra with sharp, deep grooves, with indistinct punctures, grooves unite to form pre-apical concentric pattern. Elytra crushed before their apices, apparently they are strongly bent under fully covering the tip of the abdomen from behind. Head and pronotum with fine, dense punctation, elytra without distinct punctation, punctation on underside of body fine, only mesosternum with scattered, distinct, rather coarse punctation.

122 *Dimensions.* Body length 5.5–6.0 mm, width 2.5–3.0 mm; width of head 1.2 mm; length of pronotum 1.1–1.2 mm; elytral length 3.6–4.2 mm, width 1.3–1.5 mm; length of abdomen 1.5–2.5 mm.

Comparison. Differs from type species in small size and short pronotum, from others in broad and flat tibiae.

Geotrupoides leptoscelis Nikritin, sp. nov.
(Plate X, Photo 6; Figure 66)

Species name coined from 'leptos' (Greek)—slender, and 'skelidos' (Greek)—leg.

Holotype. No. 3064/936, PIN, impression of beetle without antennae and part of legs. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Body oval. Head transverse, widest behind eyes. Pronotum transverse, its length two-thirds its width, slightly roundedly tapering before

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121 Fig. 65. *Geotrupoides sulcatus*, sp. nov.; a, b—holotype PIN No. 1668/1785: a—dorsal view, b—ventral view; c—paratype PIN No. 1989/2970, individual sclerites. Baisa, Lower Cretaceous.

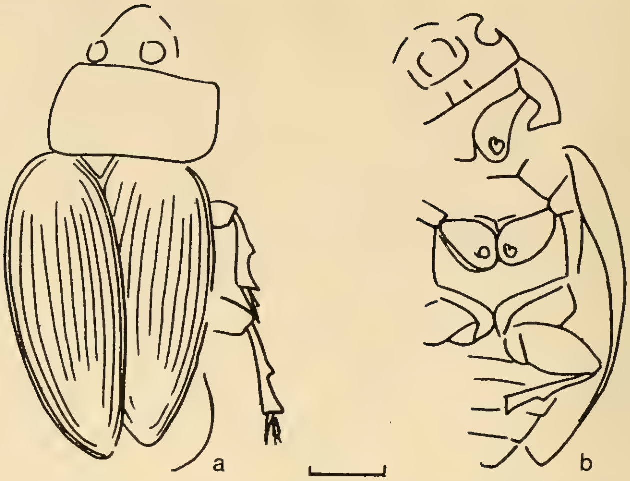

Fig. 66. *Geotrupoides leptoscelis*, sp. nov.; holotype PIN No. 3064/936: a—dorsal view, b—ventral view. Baisa, Lower Cretaceous.

middle, pronotal angles almost right-angled. Prosternum short, slightly shorter than transverse forecoxae. Mesosternum long, longer than middle coxae, its transverse suture indistinct. Mesopleura large, mesepisterna somewhat longer than mesepimera, pleural sutures oblique. Middle coxae shorter than wide, almost transverse to sternum. Metasternal length one-third its width, laterally rounded, its posterior margin angularly extending backward. Hind coxae large, not broadening laterally, its raised part running as a band along posterior margin of metasternum, extending backward along midline. Abdominal sternites almost equal in length, freely articulate. Legs rather long, femora noticeably extending beyond lateral body margins. Femora slightly uniformly broadening, hind femora slightly longer than middle femora. Middle and hind tibiae equal to femora, slender, not broadening, with longitudinal groove and one short transverse keel. Keel on the middle tibiae beyond basal third, that on hind in the middle. Tibial spurs long and slender, longer than basal tarsal segments. Elytra with sharp, slender grooves with faint punctures. Body with fine, dense shagreened punctation, mesosternum with additional large, well spaced punctures.

123 *Dimensions.* Body length 6.5 mm, width 3.0 mm; length of head 0.9 mm; length of pronotum 1.3 mm; elytral length 4.2 mm; width 1.5 mm; length of abdomen 2.3 mm.

Comparison. Differs for the type species in smaller size, and pronotum tapering toward apex, differs from other in slender legs with long tibiae and narrow grooves on the elytra.

Geotrupoides vitimensis Nikritin, sp. nov.
(Plate X, Photo 7; Figure 67)

Holotype. No. 1668/1805, PIN, impression of almost entire beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Holotype.

Description. Body broadly oval, Head transverse, widest near eyes. Labrum large, wide, anteriorly blunt. Mandibles with apical denticles, projecting from under the labrum. Length of pronotum two-thirds its width, pronotum widest in anterior third, markedly narrowing from this point anteriorly and towards base, laterally rounded. Prosternum very short, shorter than forecoxae. Mesosternum shorter than middle coxae, mesepisterna longer than mesepimera, middle coxae almost contiguous, oval, only slightly shorter than their width. Scutellum triangular, apically acutely pointed. Metasternum one-third its width, slightly narrowing anteriorly, posterior margin angularly projecting. Raised part of hind coxae gradually reduced in length laterally. Abdomen shorter than meso- and metathorax together, its sternites short, equal in length. Legs short, femora only extending up to lateral body margins. Femora rather strongly uniformly thickened; length of fore- and hind femora two times, and that of middle femora 2.5 times the width. Middle and hind femora each with two oblique rows of long hairs. Tibiae

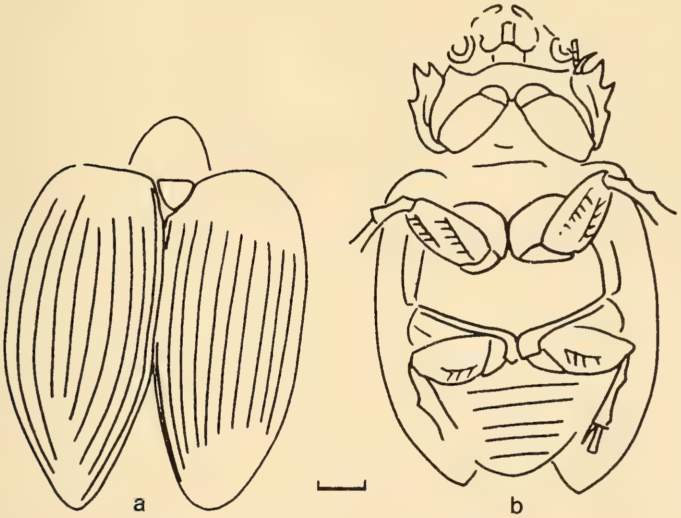

Fig. 67. *Geotrupoides vitimensis*, sp. nov.; holotype PIN No. 1668/1805: a—dorsal view, b—ventral view. Baisa, Lower Cretaceous.

approximately equal to femora in length. Foretibiae curved, flat, strongly broadening anteriorly, in anterior third with three large deticles on outer margin, and close to middle with short blunt denclicle. Middle and hind tibiae slender, apically broadening, with transverse keel close to the middle, outer margin opposite to keel projecting as broad blunt denticle. Basal segments of foretarsus short. Elytra with sharp, deep, rather broad grooves, with dis-
124 tinct punctures, grooves uniting preapically in pairs to form concentric pattern. Body dorsally almost smooth, vertrally with distinct scattered punctures, middle coxae with slightly finer punctation.

Dimensions. Body length 8.7 mm, width 4.5 mm; length of head 1.2 mm; length of pronotum 1.5 mm; length of elytra 6.2 mm, width 2.2 mm; length of abdomen 2.4 mm.

Comparison. Resembles type species in the shape of pronotum, but differs from it in smaller size, differs from other species in the shape of pronotum and structure of legs.

Genus *Proteroscarabeus* Grabau, 1923

Type species. P. yeni Grabau 1923. Lower Cretaceous of China.

Diagnosis. Large and medium-sized, broad, flattened beetles. Labrum and mandibles not fully concealed under clypeus. Pronotum transverse, laterally rounded. Spiracles of abdominal segments large, present on membrane*. Elytra not covering tip of abdomen, without distinct punctate grooves. Wings with two veins between Cubitus and the basally joining Anal.

Species composition. Type species *P. yeni* Grabau in the Early Cretaceous of China (Laiyan) and Trans-Baikal, second species in the Early Cretaceous of Trans-Baikal.

Taxonomic position. Judging from the structure of hind wings, shape of labrum, and arrangement of abdominal spiracles in membrane*, this form must be related to the lower Laparosticti, including Geotrupinae; hind wing most closely resembles wing of *Geotrupes*; a more accurate determination of its taxonomic position is difficult owing to imperfect preservation. It is probably an independent taxon of the same rank as the minor families of primitive Laparosticti.

Proteroscarabeus baissensis Nikritin, sp. nov.
(Plate XI, Photos 1–4; Figure 68)

Species named after Baisa site.

Holotype. No. 1668/1830, PIN, impression of almost entire beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

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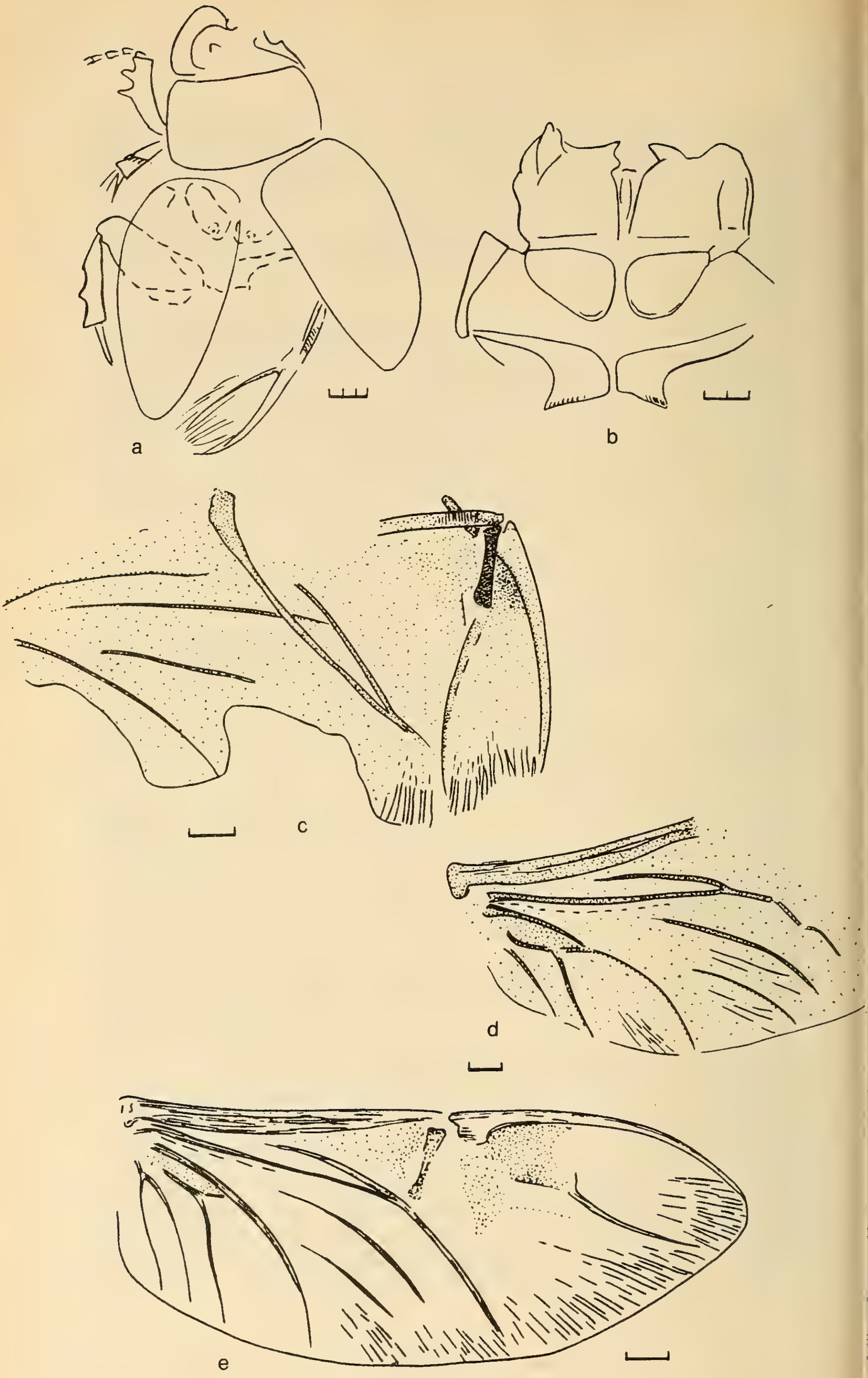
*More correctly on intersegmental membranes—General Editor.

Material. Besides holotype, isolated metathorax specimen No. 1989/2885, two incomplete hind wings specimen Nos. 1668/1761 and 3064/1072 from the same site, two isolated elytra specimen Nos. 2385/1 and 2385/5 from the Pad Semen site, Trans-Baikal, Chita oblast, Chita region, Elizabetin depression, Olengui river basin, Pad Semen, Lower Cretaceous, Argun series.

Description. Body large, broadly oval, rather thick. Head small, much narrower than pronotum, anteriorly almost not narrowing. Clypeus short, transverse, anterior border margined, medially with small tunercle. Labrum large, notably projecting from under the clypeus, anteriorly truncate, laterally rounded, mandibles strongly projecting anteriorly and laterally. Length of pronotum approximately two-thirds its width, widest in front of posterior angles whence anteriorly tapering roundly; its anterior margin emarginate, posterior margin strongly angularly extending backward, apically and at posterior angles rounded. Backward curved transverse ridge running in anterior third of pronotum. Prosternum short, forecoxae transverse. Sctutellum large, wide, transverse, rounded apically. Mesosternum transverse, noticeably shorter than middle coxae. Middle coxae convergent, ovoid, slightly oblique, almost equal in length and width. Metanotum rather long, half its width, alar cristae very sharp, scutoscutellar sutures indistinct, antenotal membranous portions absent. Metasternum very short, less than one-third its width, noticeably narrowing anteriorly, length of middle coxae 2.5 times the distance between middle and hind coxae. Metepisterna noticeably broadening anteriorly. Hind coxae large, slightly broadening
126 laterally, their raised part in medial third projecting backward, its length slightly less than width, raised part gradually tapered laterally, postero-lateral angles of medial backward projection of coxa acute, extending. Abdomen longer than meso- and metathorax together, not fully covered by elytra. Abdominal sternites approximately equal in length. Abdominal spiracles large, length of peritremes fully one-third to one-fourth the length of abdominal sternites. Spiracles not symmetrical in relation to body axis, being in a membranous fold. Legs rather long, forefemora not extending but middle and hind femora noticeably extending beyond lateral body margins. Foretibiae equal in length to femora, curved, flat and broad, with two longitudinal rows of hairs, their pre-apical width one-fourth the length. Three large denticles on outer margin in anterior half of tibiae, middle denticle somewhat larger than remaining. Hind tibiae slightly shorter than femora, flat, broadening strongly and uniformly from base to apex, with longitudinal grooves, its lateral margin beyond middle and pre-apically with blunt denticles. Spur of hind tibiae stiff, large, fully two-thirds the length of tibia itself. Foretarsi equal in length to tibiae, attached subterminally in a pit on upper


a
b
c
d
e

side of tibia, first segment slightly longer than the equal second and third, fourth longer than first, fifth longer than fourth.

Elytra convex, strongly narrowing posteriorly, apically rounded. Numerous longitudinal rows of faint punctures on elytra. Lateral third of elytra covered with pubescence, two additional narrow pubescent longitudinal bands running along elytral suture and along middle. Hind wings not very long, apical folded region approximately half the proximal region. Anterior marginal vein distinct, with spiral thickening: large sclerotized portion under it more proximal to the fold. *R* in the bent part sclerotized, wide, broadening to flexure of wing. *RS* proceeding rather sharply backward, distally curved along longitudinal axis of wing. *M* (reverse vein) reaching almost to the wing base. Two veins not joining basally with other veins present between Cubitus and first basally joining Anal vein. They are rather stiff, particularly the anterior vein, the latter not differing in thickness from other veins and basally passing close to the wing base. Surface of wing between veins corrugated in areas close to the margin. Body without distinct punctures dorsally, rough, somewhat tubercular. Metasternum along margins, especially in posterior corners, with large scattered tubercles; posterior margin of the raised part of hind coxae with sharp, transverse indentations, surface of coxae with dense distinct punctures.

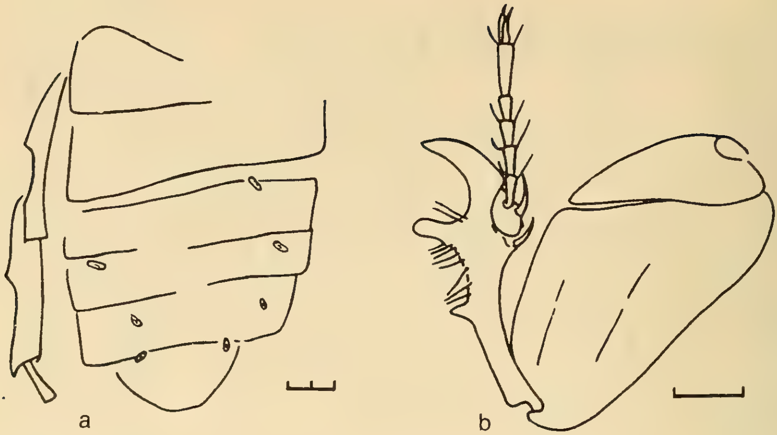
Dimensions. Body length 35 mm, width 16 mm; length of head 6 mm; length of pronotum 11 mm; length of elytra 16–17 mm, width 7–8 mm; length of wing 26 mm; length of abdomen 13 mm.

Comparison. Differs from type species in slightly larger size, and more strongly broadening hind tibiae.

Proteroscarabeus yeni Grabau, 1923
(Plate XI, Photos 5, 6; Figure 69)

Material. The stray remains of beetles resembling the holotype *P. yeni* in structure and differing from the species described above in smaller size are tentatively included in this species. These fragments include impressions of a beetle lacking a head, pronotum and a large part of the legs, specimen No. 2385/2 from the Pad Semen site, Trans-Baikal, Chita oblast, Chita region, Elizabetin depression, Olengui river basin, Pad Semen, Lower Cretaceous, Argun series. Two impressions of forelegs, specimen Nos. 1668/1797 and1989/2638 and three impressions of elytra, specimen Nos. 1989/2946, 1989/2957 and 1989/2977 from Baisa site, Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river, Lower Cretaceous, Zazin series.

Fig. 68. *Proteroscarabeus baissensis*, sp. nov.; a—holotype PIN No. 1668/1830; b—paratype PIN No. 1989/2885, c—paratype PIN No. 1668/1761, d—paratype PIN No. 3064/1072; Baisa, Lower Cretaceous, e—reconstruction of hind wing.



127 Fig. 69. *Proteroscarabeus yeni* Grabau; a—specimen PIN No. 2385/2; Pad Semen, Lower Cretaceous; b—specimen PIN No. 1989/2638, Baisa, Lower Cretaceous.

127 *Description.* Forefemora broad, less than twice as long as wide, tibiae shorter than femora, curved, broadening from base to apex. Outer margin of tibia with tuft of stiff hairs and in distal half with long denticles, two subequal apical denticles much larger than following denticles. Tarsi attached subterminally to upper surface of tibia in a pit lateral to short curved spur. Tarsi slender, basal four segments almost equal, shorter than following segment, each with a pair of apical bristles; claws straight, weak, slender.

Middle and hind tibiae slender, almost not broadening toward apex, with spines on each side. Abdominal sternites almost equal in length. Abdominal spiracles large, peritremes one-third to one-fourth the length of sternites.

Dimensions. Body length of studied specimens about 20 mm, somewhat larger than indicated for the holotype; elytral length 12–14 mm, width 6 mm; length of abdomen 11 mm.

Comparison. Distinguished by spines along lateral margins of middle and hind tibiae.

Genus *Holcorobeus* Nikritin, gen. nov.

Genus name coined from 'holkos' (Greek)—band, and genus *Scarabaeus.*

Type species. H. vittatus, sp. nov. Lower Cretaceous of Trans-Baikal.

Diagnosis. Small, broad, flat beetles. Head rather long, mandibles and labrum strongly projecting from under the clypeus. Pronotum transverse, short, laterally rounded. Elytra with indistinct punctate grooves and dark longitudinal bands, not covering tip of abdomen. Wings with large folded apical part, constituting almost half the length of the wings. *RS* parallel to anterior margin of wing, almost entire folded part without veins, only with corrugation. Claws without denticles.

Species composition. Two species in the Early Cretaceous of Trans-Baikal.

Taxonomic position. In external appearance more closely resembles May beetles than dung beetles. But, among the latter, only in Glaphyrinae are the labrum and mandibles not covered by the clypeus. *Holcorobeus* is evidently not affiliated to this subfamily since it has terminal spurs on hind tibiae. The structure of antennae and abdominal spiracles is also not known in *Holcorobeus.* Therefore its taxonomic position cannot be precisely determined, and the proposed genus should be regarded as formal.

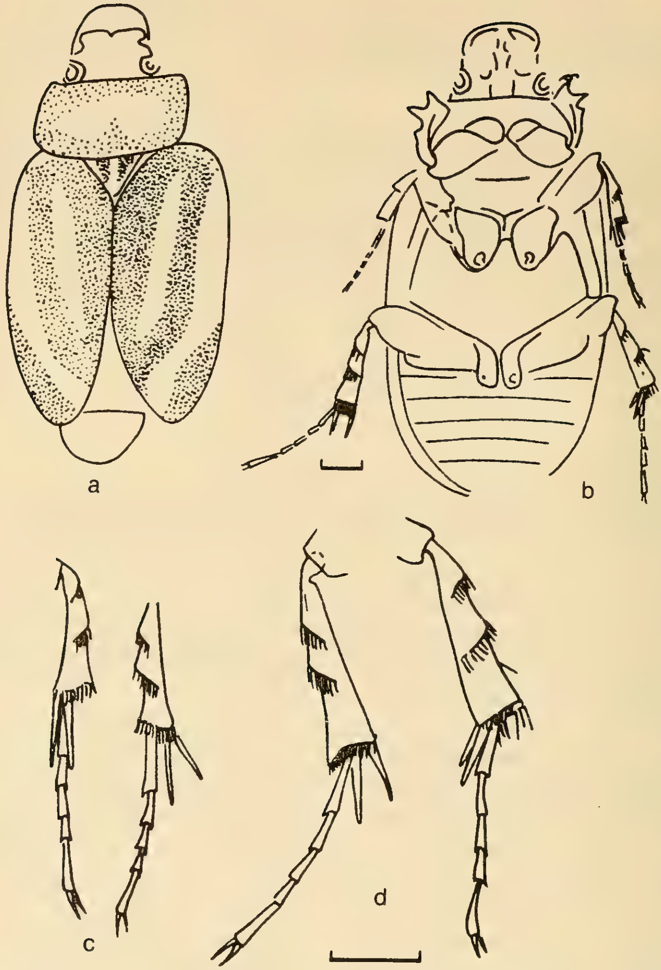
128 *Holcorobeus vittatus* Nikritin, sp. nov.
(Plate XI, Photo 7; Figure 70)

Species name coined from *vittatus* (Latin)—banded.

Holotype. No. 3064/939, PIN, impression of almost entire beetle without antennae. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Besides holotype, impression of beetle without prothorax, head and legs, specimen No. 1989/2961 and impression of isolated elytron, specimen No. 1668/1809 from the same site.

Description. Body flat, broadly oval. Head slightly shorter than its width, widest at occiput, with deep emarginations in front of eyes. Labrum long, semicircular, scarcely less than clypeus in length. Clypeus anteriorly with small border, medially narrowly emarginate, with tubercle at posterior margin. Width of pronotum 2.5 times its length, widest close to middle, uniformly narrowing anteriorly and posteriorly. Prosternum very short, much shorter than transverse forecoxae. Anterior angles of pronotum acute, slightly drawn out anteriorly, hind angles obtuse, rounded. Scutellum narrow, triangular, pointed apically. Mesosternum small, shorter than middle coxae,
129 postepisterna of mesothorax oblique, extending along inner margins of coxae anteriorly. Mesopleura large, mesepisterna and mesepimera equal in length, mesepisterna medially almost reaching the middle coxae. Middle coxae oblique, oval, apically contiguous, slightly longer than wide. Length of metasternum less than width at posterior margin strongly tapering anteriorly, posterior margin strongly angularly projecting backward, metepisterna broadening anteriorly. Abdomen shorter than meso- and metasternum together, narrowing almost from base, sternites equal in length, two-fifths of large semicircular pygidium. Legs rather short, femoral apices reaching lateral body margins. Femora uniformly broadening, forefemora two-thirds the middle and hind femora. Foretibiae noticeably shorter than forefemora,



128 Fig. 70. *Holcorobeus vittatus*, sp. nov.; holotype PIN No. 3064/939: a—dorsal view, b—ventral view, c—middle tibiae and tarsi, d—hind tibiae and tarsi. Baisa, Lower Cretaceous.

flat, anteriorly broadening, with three denticles on outer margin in anterior half; middle denticle much longer than remaining, with parallel sides and rounded apex. Middle tibiae equal to foretibiae in length, approximately half of femora, flat, broadening toward apex. Oblique transverse keel with tuft of stiff short bristles running along middle of tibia, similar tuft also present along apex. Spurs of middle tibiae scarcely longer than first tarsal segment, scarcely differing in thickness. Hind tibiae equal in length to femora, flat, strongly broadening from base to apex, divided into equal parts by two oblique transverse keels bearing tuft of stiff short bristles as at the tibial apex. Spurs of hind tibiae narrow, scarcely longer than first tarsal segment. Middle tarsi noticeably longer than tibiae, their segments slightly broadening toward apex, first tarsal segment equal to last, more than twice as long as second, second to fourth equal in length. Claws slightly curved, weak, uniform, slightly shorter than fourth tarsal segment. *Scarcely longer than tibia, segments noticeably broadening toward apices, first segment equal to fifth, one-and-a-half times longer than second, second-fourth equal. Claws markedly curved, weak, uniform, two-thirds of fourth tarsal segment. Elytra fully covering the body laterally, scarcely covering base of pygidium, bearing 12 broad, shallow grooves, with indistinct large punctures. Body with fine, dense punctation, punctures somewhat sharper on mesosternum and pygidium. Pronotum with dark-colored border, scutellum with two longitudinal dark-colored bands, elytra with dark-colored pattern consisting of broad bands along suture, bands commencing from shoulder obliquely running to sutural band and joining with it in apical third of elytron, and dark apical spot on outer margin narrow; dark-colored lines running along all punctate furrows.

Dimensions. Body length 10.5–12.0 mm, width 5.5–6.5 mm; length of head 1.9 mm; length of pronotum 1.6 mm; length of elytra 6.5–7.5 mm, width 2.9–3.2; length of abdomen 3.5 mm.

Comparison. Differs from second species in structure of tarsus and pattern on elytra, in which dark-colored bands are joined pre-apically.

Holcorobeus picturatus Nikritin, sp. nov.
(Plate XI, Photo 8; Figure 71)

Species name coined from 'picturatus' (Latin)—painted.

Holotype. No. 1989/2994, PIN, impression of beetle without head and prothorax, with unfolded elytra and hind wings. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Valanginian-Goteriv, Zazin series.

Material. Besides holotype, impression of almost entire poorly preserved beetle, specimen No. 1989/2926, and isolated elytron, specimen No. 3064/850 from the same site.

Description. Body flat, oval. Length of head markedly less than width, in front of eyes with shallow narrow emarginations. Length of pronotum two-fifths its width. Forecoxae transverse, with blunt keel. Scutellum triangular, slightly longer than wide. Middle coxae elongate along body, contiguous to a large extent apically, slightly longer than wide. Length of 130

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*Translation of the following sentence correct. Apparently the words 'Hind tarsi' missing in the Russian original. Otherwise the sentence does not make any sense—General Editor.

metasternum one-third the width at posterior margin, strongly narrowing anteriorly, posterior margin slightly extending backward. Abdomen shorter than meso- and metathorax together, tapering from base of third sternite. Femoral apices noticeably extending beyond lateral body margins. Femora broadening, fusiform. Foretibiae shorter than femora, flat, with a rather large blunt denticle in anterior third, more proximal to it and apically with small denticles. Middle tibiae short, much shorter than femora, flat, broadening toward apex. Oblique keel with tuft of short stiff bristles present in distal third; similar tuft but with much larger bristles at broad apex of tibia. Spurs of middle tibiae narrow, slightly longer than first tarsal segment. Hind tibiae shorter than femora, broadening in apical third with transverse oblique keel and with tuft of stiff hairs as at apex. Spurs of hind tibiae large, flat, cultrate, fully half the length of tibiae, slightly longer than first tarsal segment. Middle tarsi scarcely longer than tibiae, their segments noticeably broadening toward apex, first segment three times as long as second, second to fourth segments equal, last two-thirds of first. Claws uniform, curved, equal to fourth tarsal segment. Hind tarsi longer than tibiae. Elytra without noticeable grooves. Body with fine punctation. Elytra with dark-colored, posteriorly narrowing band along suture and slightly oblique band running from shoulders to apex.

Dimensions. Body length 9.5–10.5 mm, width 4.5 mm; length of head 1.8 mm; pronotum 1.2 mm; elytra 6.6 mm, width 2.8 mm; length of wing 12.0 mm; length of abdomen 4 mm.

Comparison. Distinguished by structure of tibiae and tarsi and elytral pattern consisting of parallel dark-colored bands.

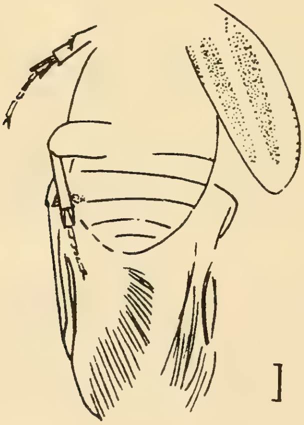

Fig. 71. *Holcorobeus picturatus*, sp. nov.; holotype PIN No. 1989/2994. Baisa, Lower Cretaceous.

INFRAORDER ELATERIFORMIA

SUPERFAMILY CEBRIONOIDEA LATREILLE, 1802 (= Elateroidea Leach, 1815)[1]

Family CEROPHYTIDAE Latreille, 1834

This family includes a single extant genus *Cerophytum* Latr. with several species from western Europe, North and Central America. Fossil representatives of Cerophytidae were not known until now. As it turns out, remains of these beetles are frequently encountered in the Cretaceous fossil resins of Siberia.

Based on several distinguishing characters, the Cretaceous genus *Aphytocerus* described below may be considered less advanced than the extant *Cerophytum.* In *Aphytocerus* the antennae are only slightly serrate even in the male (i.e., the process of increasing the surface of their segments had only just commenced), whereas *Cerophytum* males possess highly serrate antennae. The development of serrate antennae is usually associated with complicated sensory apparatus. Further, in *Aphytocerus* the femoral 131 plates still exist, although greatly reduced in comparison with many other Cebrionoidea. They are completely absent in *Cerophytum,* which Crowson (1955) explains by the necessity to increase the surface area of the femora in connection with the development of the springing ability. In *Aphytocerus* the hind femora do not exhibit any characters for this purpose. The slightly oblique articulation of the trochanters with the femora, distinguishing *Cerophytum* from other Cerbrionoidea, is probably a secondary phase which *Aphytocerus* also has not reached. Moreover, many apomorphs common to *Cerophytum* and *Aphytocerus* (marked elongation of trochanters, development of antennal sockets, flattening of hind coxae, and others), must have already been formed before the Late Cretaceous. However, *Aphytocerus* has several autapomorphs which prevent its consideration as an ancestor of *Cerophytum* (head deeply retracted into prothorax, spinescent prosternal process). *Aphytocerus* is undoubtedly an extinct specialized branch of the family Cerophytidae.

Some postulations can be made on the ecological characteristics of *Aphytocerus* and the direction of its specialization. As far as is known, species of the genus *Cerophytum* in Europe and North America live under the bark of dead trees and in decomposing wood. This is probably the original mode of life for Cerophytidae. In its general habits *Aphytocerus* somewhat resembles Anobiidae, living in dry, dead wood and preferring dead knots on living trees. Inhabitants of decomposed wood are rather uncommon in fossil resins. They apparently occur by chance, since repeated finds of any particular species are rare. Species inhabiting living trees are far more common in resin. *Aphytocerus* is observed in resin very frequently. It is present in a small volume of material of the Senomanian resins from the Ust'-Yenisey basin, while in the collection of Cognacsantonian resin from the Khatang basin it is represented by seven specimens, constituting 25% of the total number of beetles. Therefore it is highly likely that *Aphytocerus* inhabited the same species (or several species) of conifers which produced the resins containing their remains. Unfortunately, there is still no information on the taxonomic status of these conifers; judging from the composition of the spore-pollen conglomerates, Cupressaceae and/or Taxodiaceae as well as Pinaceae and *Pinus* in particular were predominant among conifers in Taimyr at that time (Saks et al., 1959). The development of *Aphytocerus* probably took place in dead knots of trees at the base of which resin secretion is frequently observed in the extant conifers; this mode of life was definitely most suited for burial.

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[1] The name Elateroidea Leach, 1815, suggested by Leng (1920) must be replaced by the available priority name Cebrionoidea Latreille, 1802, nom. trans. hic ex Cebrionides Latreille, 1802.

Genus *Aphytocerus* Zherichin, gen. nov.

Genus name coined from genus *Cerophytum.*

Type species. Aphytocerus communis, sp. nov. Upper Cretaceous of Taimyr.

Description. In general body shape this species resembles representatives of the family Anobiidae; covered by sparse short hairs.

Head markedly retracted into prothorax and bent under it, dorsally almost not visible. Eyes large, rounded, occupying large part of visible surface of head. Antennae ten-segmented, attached to frons between eyes in deep, wide, rounded sockets; their inner margins continuous while outer margins directly bordering the eyes. Distance between antennal bases almost equal to the length of their first segment. Antennae fairly long, extending beyond base of elytra, weakly serrate; their first segment very large, apically truncate, last segment slender, longer than penultimate. Antennae slightly shorter in males than in females and more strongly serrate. Maxillary palps short with dolabriform broadening of last segment. Mouth parts at rest covered by anterior hood of pronotum and not visible.

Protonum transverse, companulate, highly convex, rounded laterally. Convexity of pronotum not same all over; highest in anterior half, pronotum
132 hanging somewhat like a hood over the head. Posterior angles of pronotum drawn out into short cusps, its base with two emarginations. Pronotum at anterior margin with distinct hood, with pronounced, rather deep, arcuate longitudinal grooves for insertion of antennae. Posterior margin of prosternum extending into narrow point, inserted into mesosternal depression and almost reaching midpoint of middle coxae. Scutellum large, wide, flat, apically rounded.

Elytra elongate, almost cylindrical, with angularly projecting shoulders and distinct humeral tubercle, apically broadely rounded, fully covering abdomen. Basal margin of elytra arcuate, rounded. Lateral margins almost parallel, in side view with sharp S-shaped bend at the level of hind coxae. Punctate grooves regular, with distinct and rather deep punctures; last groove truncate, reaching only up to hind coxae.

Mesosternum very short, with depression for insertion of prosternal process. Metasternum large, slightly convex, with small medial groove at posterior margin.

First abdominal sternite short, following three of same length, slightly longer than first and weakly convex. Fifth sternite nearly as long as fourth, flat, apically rounded, without pits or elevations. Sutures between sternites straight.

Forecoxae rounded, convergent, separated only by narrow prosternal process. Middle coxae the same size, spherical, protuberant, convergent, distance between them about one-third of their diameter. Hind coxae strongly transverse, almost completely flat, with small femoral plates. Trochanters very large, obliquely articulate with femora, their length in fore- and middle legs about one-third and in hind legs one-half of the femoral length. Femora weakly clavate, with subapical constriction and notch for articulation; forefemora* almost round in cross section, slender, in length nearly equal to femora plus trochanters, in apical half covered by rather long (only slightly shorter than tibial diameter), slender, vestigial hairs, with two slender, short apical spurs on inner side. First tarsal segment cylindrical, long; second and third equal in length, half the length of first, more or less triangular; fourth somewhat longer and much wider than third, flattened; fifth long and slender, thickening apically, attached in depression on inner side of fourth segment. Foretarsi slightly broadening in male. Claws slender, long almost half the length of tarsal segment, slightly curved, with weak, blunt basal denticle.

Species composition. Two species in the Late Cretaceous of Taimyr.

Comparison. Differs from sole earlier known genus *Cerophytum* in serrate (not pectinate) antennae of male, presence of femoral plates (though reduced) on hind coxae, oblique articulation of trochanters with femora, head deeply retracted into prothorax, and narrow and angular (bit not rounded) prosternal intercoxal process.

Remarks. The combination of characters such as serrate ten-segmented antennae, rounded forecoxae, grooves for insertion of antennae, posterior prosternal process, strongly transverse and almost contiguous hind coxae with femoral plates, absence of transverse suture on metasternum, five-segmented tarsi, and the trilobate male genitalia make it possible to confidently include *Aphytocerus* under Cebionoidea. Exceptionally long trochanters; flat

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*An obvious misprint in the Russian original. Logically should refer to tibiae—General Editor.

hind coxae; elongate first and broad fourth tarsal segment; first segment of antennae enlarged, inserted in large, closely convergent sockets between eyes, and presence of small pronotal hood are characteristic in this superfamily only of Cerophytidae; the latter is a small independent group, sharply differing from the other families in several characters. R. Crowson (1955), in the diagnosis of the family Cerophytidae describes several atypical charcters of *Aphytocerus* (such as slightly oblique articulation of trochanters
133 with femora and total reduction of femoral plates of hind coxae). Since this diagnosis is based on a single extant genus, it is not surprising that the find of a second genus necessitates a certain alteration in the diagnosis.

Aphytocerus communis Zherichin, sp. nov.
(Plate XII, Photo 1; Figure 72, a–e)

Species name coined from 'communis' (Latin)—common.

Holotype. No. 3311/41, PIN, male, a fully preserved beetle embedded in fossil resin (retinite). Taimyr national district, Khatang region, Yantardakh area on the right bank of Maimechi river 5 km upstream from its mouth (Yantardakh site). Upper Cretaceous, Gognac-Santon, Kheta series.

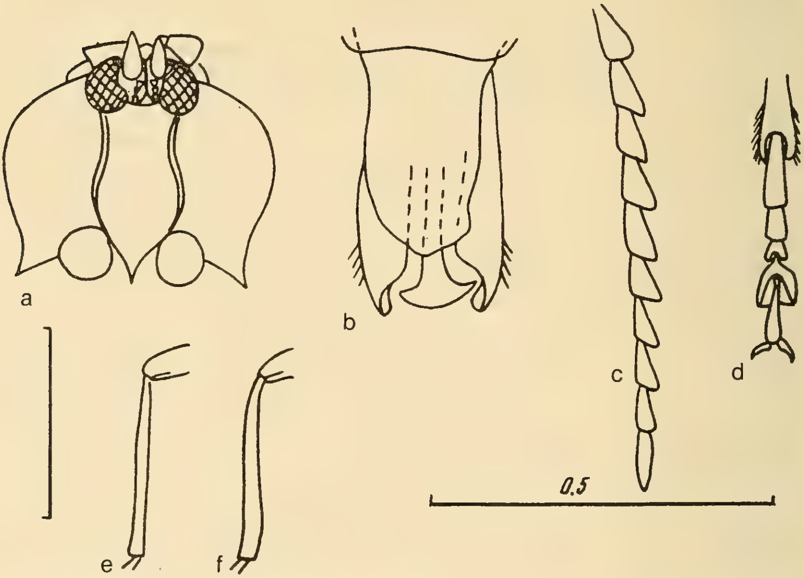

Fig. 72. Representatives of genus *Aphytocerus*: a to e—*A. communis*, sp. nov.; holotype PIN No. 3311/41: a—head and prothorax, b—genitalia, c—antenna, d—tarsus, e—hind tibia; Yantardakh, Upper Cretaceous; f—*A. dolganicus* sp. nov.; holotype PIN No. 3426/35, hind tibia; Agapa, Upper Cretaceous.

Material. Besides holotype, six more or less damaged and incomplete remains from the same site, specimen Nos. 3130/28, 3130/29, 3130/35, 3311/42, 3311/43, 3311/44.

Description. Color of body black. Eyes, palps, antennae, apices of forefemora, middle and hind trochanters and femora, all tibiae and tarsi light yellowish-brown, first segment of antennae and middle of middle and hind legs dark colored. Head, pronotum, elytra, and thorax covered with very dense and minute, almost pollinose, fine hairs; abdominal sternites with rather long and very slender, contiguous, whitish hairs.

Frons anterior to antennal sockets with fine, dense punctation. Antennae in male extending beyond humeral tubercles of elytra, distinctly serrate, dorso-ventrally flattened. Their first segment broad, oval, slightly longer than wide; following five segments similar, triangular, almost equal in length and width; seventh and eighth of the same length but narrower, with less projecting apical corners; ninth equal in length to eighth, oval; tenth noticeably narrower and somewhat longer than ninth, slightly pointed apically. Antennae of female more slender and longer, reaching the level of hind coxae. Their segments narrower and more elongate, with less projecting corners, but also
134 flattened; length ratios of segments approximately the same as in the male. All antennal segments densely covered with short and slender hairs.

Pronotum widest in middle, equal in width to elytra, width 1.25 times the length, with small lateral depression in front of hind corners, depression deeper in male, posterior angles directed backward, somewhat laterally and upward. Sculpture formed by very dense, fine punctures, distance between which almost equal to their diameter; pattern very fine-grained laterally.

Ratio between elytral length and width 14 : 9. Sides of elytra behind anterior third with small but distinct depression. Punctures in grooves elongate, distance between punctures considerably less than their length; intervals between punctate grooves narrow, equal in width to grooves but laterally narrower and very finely shagreened. Lower side of thorax, coxae, femora, trochanters and abdominal sternites with very fine, dense, uniform punctures, distance between which nearly equal to their diameter. All tibiae straight. Genitalia as in Plate XII, Photo 1b; Figure 72b.

Dimensions. Body length 2.6–3 mm.

Comparison. Distinguished by denser, elongate punctures in elytral grooves and straight hind tibiae.

Aphytocerus dolganicus Zherichin, sp. nov.
(Figure 72f)

Species named after Dolgan nationality.

Holotype. No. 3426/35, PIN, male, split into two parts, and partially oxidized inclusion of beetle in fossil resin (retinite), apex of elytra not preserved. Taimyr national district, Ust'-Yenisey region, Lower Agapa river, 40 km downstream from its mouth (Agapa site). Upper Cretaceous, Senomanian, Dolgan series.

Material. Holotype.

Description. As far as can be judged from the preserved fragments of integument, the body color is black. Antennae and legs (except coxae) entirely light yellowish-brown. Pubescence as in *A. communis.*

Antennae in male reaching the level of hind coxae, distinctly serrate, dorso-ventrally flattened. Their first segment broad, oval, longer than wide; following four segments similar, triangular, somewhat longer than wide; sixth, seventh and eighth segments the same length, slightly narrower, with less projecting apical corners; ninth segment oval, equal in length to eighth; tenth almost negligibly narrower and longer than ninth.

Pronotum widest at middle, equal to elytra in width, width 1.25 times the length, laterally uniformly rounded, anterior to posterior angles with shallow depression. Sculpture formed by very dense, fine punctures, distance between punctures in the middle of pronotum slightly more than their diameter but almost equal on sides near posterior margin.

Elytra, behind anterior third, with lateral depressions of apparently about the same proportions as in *A. communis*. Punctures in grooves round, distance between them 1.5–2 times their diameter. Intervals between punctate grooves narrow, nearly one-and-a-half times broader than grooves, but laterally equal to them in width, and finely shagreened. Lower side of thorax, coxae, femora, trochanters and abdomen with very fine, dense, uniform punctures. Fore- and middle tibiae straight, hind tibia distinctly curved in apical third. Structure of male genitalia not known since, although preserved even in the holotype, they are highly oxidised and the structural details are not discernible.

Dimensions. Body length 3.3 mm.

Comparison. Close to *A. communis*, differs from it only in larger size, entirely light-colored legs, long antennae of male, round and sparser punctures in elytral grooves, and curved hind tibiae.

135 SERIES OF SUPERFAMILIES OF CICUJIFORMIA

SUPERFAMILY CLEROIDEA LATREILLE, 1802

Family ACANTHOCNEMIDAE Crowson, 1964

This family was established for a single Recent genus *Acanthocnemus* Perr. and until that time was unknown as a fossil. Initially it was given the rank of a subfamily (Crowson, 1964), but later of a family (Crowson, 1970) based on a study of larvae tentatively identified as *Acanthocnemus.* The mode of life of Acanthocnemidae is almost unknown. Crowson (1970, p. 19) suggests that they are affiliated to the main line of "more or less predatory" cleroids, but pollen also forms an important food for several members of other families in this branch. The young larva was found in soil under the roots of eucalyptus and is apparently a predator.

Acanthocnemidae is morphologically one of the most archaic groups among Cleroidea and probably one of the most ancient families of this superfamily. The extant genus *Acanthocnemus* Perr., judging from its isolation and unique geographic distribution, is a very ancient relict. According to G.G. Yakobson (1905–1915) and G. Champion (1922) only one species *A. nigricans* (Hope) belongs to this genus, and has been repeatedly described under different names. The geographic distribution of this species covers Australia, Tasmania, New Caledonia, Burma, Thailand, India, Madagascar, South Guinea, Algeria, Sicily, Sardinia, Corsica and Cyprus. Champion considers Australia to be its native habitat and suggests that it has been introduced into other parts of the world. However, *Acanthocnemus* has apparently never been noted in ships or in transported goods. It does not occur solely in the Port areas, nor has it been found even once in the western hemisphere. Therefore one may suspect that *A. nigricans* inhabits a very wide but distinctly discontinuous natural geographic area; probably, it existed as a species for a very long time, at least since the Early Paleogene. Examples of such ancient species, though very few, do occur among insects. In some instances, the habitats of present-day species of terrestrial arthropods resemble, to some extent, the habitat of *A. nigricans*, for example, those of the Protura (Tuxen, 1967).

Genus *Acanthocnemoides* Zherichin, gen. nov.

Genus name coined from *Acanthocnemus* Perr.

Type species. Acanthocnemoides sukatshevae, sp. nov. Upper Cretaceous of Taimyr.

Description. Body somewhat flat, resembles members of the Malachiinae (Melyridae) in general appearance. Uniformly covered with moderately dense, thick, erect bristles. Integument apparently rather soft, but not to the same extent as in the Malachiinae.

Head broad, its width (with eyes) greater than length. Eyes large, rounded, highly convex, extending far beyond the margin of head. Frons broad, only slightly narrower than anterior margin of pronotum. Clypeus simple, triangular. Temples long, nearly half the length of eyes. Mandibles with two apical denticles. Maxillary palps with triangular segments broadening toward apex and last segment terminally truncate. Labial palps short, last segment dolioform. Antennae slender and rather long, extending beyond base of elytra, attached in front of eyes at a very short distance from them. All antennal segments longer than wide; last three segments flattened and broadened, forming a very loose but distinct club.

Pronotum transverse, with strongly rounded sides and distinct, rather broad (particularly in posterior half), flat lateral margin. Posterior margin of 136 pronotum slightly wider than anterior, straight. Disk of pronotum weakly convex. Prosternum without a depression in front of forecoxae, only with very indistinct transverse fold. Scutellum triangular, weakly transverse.

Elytra long, ovoid, basally slightly broader than base of pronotum, smoothly broadening posteriorly, widest behind midlength, apically broadly rounded. Shoulders projecting, rounded, humeral tubercle nearly undeveloped. Epipleura broad at base, posteriorly narrowing, disappearing at level of hind coxae.

Mesosternum very short, convex, its narrow pointed intercoxal process almost reaching posterior margin of coxae. Metasternum long, weakly convex, without depression or grooves; at anterior margin between coxae with broad, short and flat, apically rounded projection; posterior margin of metasternum arcuate. Abdominal sternites almost flat, similar, last sternite in both sexes without pit or processes, broadly rounded at apex.

Forecoxae large, projecting, strongly convergent, distance between them almost equal to tibial* width. Forecoxal cavities broadly open posteriorly. Middle coxae rounded, convergent, separated only by narrow mesosternal process. Hind coxae strongly transverse, contiguous, without femoral plates. Legs slender and long. Trochanters rather large, obliquely articulating with bases of femora. Femora long, slightly thickened toward apex. Tibiae slender, equal in length to femora, outer margin without spines, inner margin with row of short and thick erect bristles; [tibiae] straight, in females hind tibiae slightly S-shaped. Tarsi equal to tibiae in length, slender, five-segmented, with long cylindrical segments and long, slender, simple claws. Last tarsal segment 1.5 times longer than penultimate. Foretarsi of same structure in male and female. Hind tarsi slightly longer than other tarsi.

Species composition. One species from the Cretaceous of Taimyr.

Comparison. Differs markedly from the single earlier known genus (*Acanthocnemus* Perr.) in the triangular (not cylindrical) last segment of maxillary palps; elongate (not transverse) fourth to eighth antennal segments; long, posteriorly broadening temples; ovoid (not parallel-sided) elytra; absence of pit on prosternum and row of spines on outer margins of tibiae; shorter last tarsal segment, and identical structure of foretarsi in males and females.

Remarks. This genus definitely belongs to the superfamily Cleroidea. This is confirmed by the general appearance of the beetle and by the projecting forecoxae, lack of plates on hind coxae, and structure of antennae

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*So given in the Russian original. Earlier the intercoxal distance was always compared with coxal and not tibial size, hence the doubt—General Editor.

and tarsi. The identification of the family is a somewhat more complicated problem. Crowson (1970) characterizes the Acanthocnemidae by the following structural features of the imago, which differentiate them from the Melyridae: antennae with distinct three-segmented club; claws simple; outer margin of tibiae with short, thick spines; prosternum with paired pits in front of coxae; and edeagus with divided phallobase*. Of these characters, the first two are observed in *Acanthocnemoides* but not next two; the structure of the phallobase could not be determined from the available material. However, based on these two characters, *Acanthocnemoides* is closer to Melyridae. Crowson seems to attach little importance to the prosternal pit since he states "the first acanthocnemoids were possibly without prosternal pits" (Crowson, 1970, p. 19). The armature of the tibiae also seems to be an unimportant character, and hence *Acanthocnemoides* is here assigned to the Acanthocnemidae with which its proximity cannot be doubted. The Acanthocnemidae may be better ranked as a subfamily of Melyridae. However, this question cannot be adequately resolved in the absence of material on Recent *Acanthocnemus*.

137 *Acanthocnemoides sukatshevae* Zherichin, sp. nov.
(Plate XII, Photo 2; Figure 73)

Species name after I.D. Sukacheva, who collected the material.

Holotype. No. 3308/1, PIN, female, inclusion of an entire beetle in retinite (split during study); Taimyr national district, Khanag region, right bank of Zhadnikha river at its source (Zhadnikha site). Cretaceous, Albian ?—Senomanian, Begichev series (middle member).

Material. Besides holotype, one specimen (male), specimen No. 3308/2 slightly damaged, from the same site; found in the same lump of retinite as the holotype.

278 *Description.* General coloration of body dark, blackish-brown; palps, antennae and legs light-brown, last two segments of antennae black. Entire body uniformly densely covered with fine, rather long, dark-colored, oppressed pubescence.

Head with fine, uniform punctation. First antennal segment large, strongly thickening apically. Second slightly narrower than first, but wider than subsequent segments, short, ovoid, slightly compressed dorsoventrally. Following three segments of the same shape and size, slightly broadening toward apex, not flattened, twice as long as wide; sixth segment of the same width but slightly shorter, 1.5 times longer than wide; seventh 1.5 times longer and slightly wider than sixth; eighth of the same size and shape as the sixth. All these segments, except the first two, with whorls of fine hairs on

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*Although the Russian original uses the term "tegmen" we prefer to use the more current term "phallobase"—General Editor.

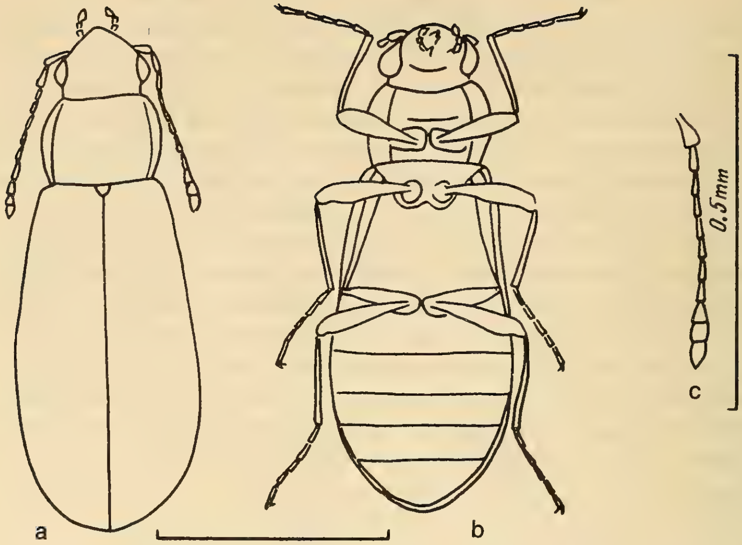

Fig. 73. *Acanthocnemoides sukatshevae*, sp. nov.; holotype PIN No. 3308/1: a—dorsal view; b—ventral view; c—antenna. Zhadnikha, Cretaceous.

the broadened apical part. Ninth and tenth segments twice as wide as eighth, dolioform, longer than wide; eleventh a little wider and longer than tenth, apically pointed. All segments of club with rather long, sparse hairs.

Length of pronotum two-thirds its maximum width, and with fine, dense, uniform shagreening. Pubescence directed posteriorly slightly longer on sides than on disk. Elytra twice as long as maximum width, uniformly finely shagreened, without grooves; pubescence on elytra directed posteriorly. Thorax on ventral side and abdomen with similar shagreening.

First three segments of foretarsi equal, cylindrical, three times longer than wide; fourth segment of same length but considerably thinner; fifth 138 equal in length to the preceding two together. First four tarsal segments ventrally with stiff bristles. Middle tarsi of same structure; hind tarsi with slightly longer segments, their length ratios same as in fore- and middle tarsi.

Only narrow apex of edeagus visible in paratype (male).

Dimensions. Body length 2.2 mm.

INFRAORDER CUCUJIFORMIA LATREILLE, 1802

Family CRYPTOPHAGIDAE Erichson, 1845

Subfamily Atomariinae Leconte, 1862

Genus *Nganasania* Zherichin, gen. nov.

Genus named after the Nganasan nationality.

Type species. Nganasania khetica, sp. nov. Upper Cretaceous of Taimyr.

Description. Body slightly flattened dorsoventrally, with fine hairs. Head considerably narrower than pronotum, transverse. Eyes large, rounded, moderately convex, projecting beyond margin of head. Temples absent. Antennae freely [= movably] attached to anterior part of frons in front of eyes, rather long and thick, reaching humeral tubercles of elytra; basal segments of antennae thickened, first segment longer and broader than second; antennal club loose, three-segmented.

Pronotum weakly transverse, in lateral view appearing to form a common flat arc with elytra, not delineated from the latter by a drop-off. Sides of pronotum almost parallel in posterior half, converging anteriorly, without denticles of projections. Widest part of pronotum is its weakly bicrenate base. Anterior angles of pronotum not projecting, without depression; posterior angles slightly projecting laterally; pronotum lacking discrete lateral margin. Disk of pronotum with smooth ornamentation, without keel or depression. Forecoxal cavities open posteriorly. Scutellum large, clearly visible, equal in length and width, flat, pentagonal.

Elytra almost parallel-sided, basally slightly wider than pronotum, with slightly projecting shoulders, posteriorly bluntly tapering, fully covering abdomen. Sculpturing on elytra consisting of small punctures, not forming distinct rows; presutural row of punctures apparently rudimentary but impossible to confirm in our material. Epipleura of elytra developed in basal half, rather wide, disappearing further on.

Mesothorax short, sloping backward, but not vertically; metathorax long. Abdominal sternites weakly convex; third and fourth sternites of same length; structure of first and second not known; fifth flat, rounded at apex.

Forecoxae transverse, projecting, closely convergent. Middle coxae strongly convergent, rounded. Hind coxae small, triangular, closely convergent. All trochanters large. Femora moderately thickened. Tibiae slender, straight, equal in length to femora; foretibiae apically with two slender indistinct spurs. All tarsi five-segmented (? female), their first four segments identical in shape, simple, not bilobed; fifth segment long, equal in length to the preceding three together; claws simple, slender and short.

Species composition. Monotypic genus.

Comparison. Apparently very close to the extant genus *Ootypus* Ganglb., but differs in pubescent integument. Also resembles *Atomaria* Steph. but differs in the lack of a drop-off between the pronotum and elytra, and by the pronotum not narrowing posteriorly.

Remarks. The affiliation of *Nganasania* to Cryptophagidae has been reliably established from a complex of distinguishing characters (structure 139 of antennae and tarsi; converging coxae; posteriorly open forecoxal cavities; long trochanters; presence of two spurs on foretibiae; epipleura of elytra disappearing in posterior half, and to the subfamily Atomariinae from the antennae freely [= movably] attached to the anterior part of frons. In its general evolutionary level, *Nganasania* does not differ from the extant Atomariinae, nor does it show any plesiomorphic features. The present-day representatives of this group occupy various cryptic habitats ([forest] litter, decomposing wood, burrows and nests of animals); they feed primarily on mold fungi, rarely on plant shoots.

Nganasania khetica Zherichin, sp. nov.

(Plate XII, Photo 3; Figure 74)

Species name coined from Kheta series.

Holotype. No. 3311/45, PIN, inclusion of an entire beetle in fossil resin (retinite); partially hidden by detritus and opacities in the resin. Therefore, it was not possible to identify some structural details (particularly of the ventral side). Sex could not be determined. Taimyr national district, Khatanga region, Yantardakh area on right bank of Maimechi river, 5 km upstream from its mouth (Yantardakh site). Upper Cretaceous, ? Kon'yak-Santonian Kheta series.

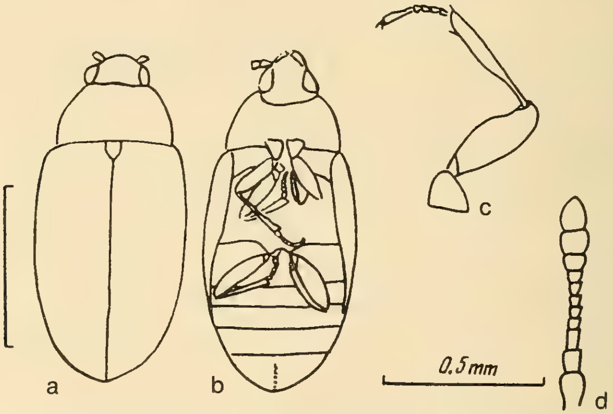

Fig. 74. *Nganasania khetica*, sp. nov.; holotype PIN No. 3311/45: a—dorsal view; b—ventral view; c—foreleg; d—antenna. Yantardakh. Upper Cretaceous.

Material. Holotype.

Description. Coloration of body rusty-brown, epipleura of elytra slightly lighter in color; pubescence short and fine, dark-colored. Bases of antennae widely spaced, separated from each other by length of their first segment, and from anterior margin of eyes by distance equal to half the diameter of eyes. First antennal segment twice as long as wide; second segment slightly thinner and three-fourths the length of first; third segment half as thick as second, considerably longer than wide; following four segments alike, more or less cylindrical, of same thickness but considerably shorter than third, equal in length and width. Eighth segment of same length and width as preceding segments, almost spherical. Ninth twice as wide as eighth, equal in length and width almost square; tenth slightly wider than ninth, equal in length and width, slightly broadening apically. Eleventh of same width as tenth, slightly longer, symmetrical, pointed apically.

Pronotum one and a quarter times wider than long, and weakly shagreened. Elytra three times as long as pronotum, with fine punctures and weak shagreening. Lower side of body with similar ornamentation. Last abdominal sternite with longitudinal groove. First four segments of tarsi slightly longer than wide.

Dimensions. Body length 2.0 mm.

140 Family LATHRIDIIDAE Redtenbacher, 1845

Subfamily Corticariinae Stein, 1877

Genus *Succinimontia* Zherichin, gen. nov.

Genus name coined from 'succinum' (Latin)—amber, and 'mons' (Latin)—mountain (Latin translation of the locality name Yantardakh).

Type species. Succinimontia infleta, sp. nov. Upper Cretaceous of Taimyr.

Description. Body elongate, slightly flattened. Head broad, transverse, narrowing anteriorly, together with eyes narrower than anterior margin of pronotum. Eyes rounded, strongly convex, almost hemispherical. Temples absent. Frons flat, without keels or tubercles. Fronto-clypeal suture distinct, but shallow. Clypeus and frons coplanar. Antennae 11-segmented; third to fifth segments round, equal in length and breadth; sixth to eighth segments weakly transverse; club loose, three-segmented, its apical segment symmetrical, pointed.

Pronotum transverse, wider in anterior half, posteriorly narrowing, with weak denticles at sides. Posterior margin of pronotum slightly arched, convex. Disk of pronotum without keels or longitudinal depressions; basal pit absent, only a very flat [shallow] depression present, occupying entire base. Scutellum clearly visible, comparatively narrow, equal in length and width, without pits, grooves, keels or folds; flat.

Elytra noticeably broader than pronotum, with rounded sides, ovoid, broadest beyond middle, rounded apically, with rows of punctures. Intervals between grooves without keels or projections. Development of pubescence on elytral integument unclear; if present, then composed of poorly noticeable short hairs. Humeral tubercles distinct, projecting, depression present between them and lateral margin.

Forecoxal cavities posteriorly closed. Abdomen with five visible sternites. Projection of first sternite between hind coxae wide, flat, arcuate. First sternite long, equal in length to the following two together, without femoral lines. Second and third sternites equal in length, fourth slightly shorter; sutures between sternites straight. Fifth sternite longer than fourth, apically rounded, flat, without depressions or tubercles.

Forecoxae contiguous, middle and hind coxae wide-set. Trochanters short, almost equal in length and width, obliquely articulating with femora. Femora weakly clavate, rather broad. Tibiae straight, wide, flattened, slightly longer than femora, their inner margin with small preapical enlargement, without denticles. Tarsi three-segmented, considerably shorter than tibiae, their first segment longer than broad and distinctly longer than second; third segment equal in length to the preceding two together, slender. Claws simple, slender, short.

Species composition. Monotypic genus.

Comparison. Most closely resembles the present-day genus *Corticarina* Reitt., from which it differs in the transverse segments of antennae, absence of a distinct pubescence on elytra, and five visible abdominal sternites. Differs from the genus *Melanophthalma* Motsch. in the absence of femoral lines on the first [abdomen] sternite and narrower scutellum without folds and grooves; from *Corticaria* Marsh. it differs in the slightly serrate lateral margin of pronotum and narrower scutellum; from *Migneauxia* Duval in the 11-segmented antennae, elongate body and longer first tarsal segment; from Cortilena Motsch. and *Diarthrocera* Broun* in the three-segmented antennal club.

Remarks. Succinimonitia definitely belongs to Lathridiidae. It is a very typical representative of the family, fairly similar to the present-day forms, and the combined characters relegate it to the rather advanced subfamily Corticariinae. Ecologically *Succinimontia* hardly differs from the extant
141 *Corticaria, Corticarina* or *Melanophthalma* to which it is most closely related. Representatives of this group inhabit shelters, particularly in the forest litter and other heaps of plant detritus, sometimes under the bark of dead wood, in burrows and nests of different animals, etc.; they feed on mold fungi.

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*Author's name could not be confirmed—General Editor.

This genus is the first Mesozoic representative of the family Lathridiidae.

Succinimontia infleta Zherichin, sp. nov.
(Plate XII, Photo 4; Figure 75)

Species name coined from 'infleta' (Latin)—unwept.

Holotype. No. 3130/31*, PIN, inclusion of almost entire beetle in retinite, sex not determined. Taimyr national district, Khatanga region, Yantardakh area on right bank of Maimechi river, 5 km upstream from its mouth (Yantardakh site). Upper Cretaceous, ? Cognac-Santonian, Kheta series.

Material. Holotype.

Description. Color brown, antennae and legs slightly lighter.

Interorbital width of frons twice the diameter of eyes, finely shagreened. First antennal segment strongly clavate, its length twice its width, width of second half the apical width of first and half its length, almost cylindrical, very slightly broadening apically; ninth twice as long as eighth, ovo-triangular, equal in length and width; tenth of same length and width as ninth, rounded; eleventh 1.7 times longer than wide, parallel-sided, almost rectilinearly tapering anteriorly in apical third.

Pronotum one-third wider than long, rounded laterally, without sharply projecting corners, only with small denticles arranged as follows: two comparatively strong, pointed, triangular denticles in the anterior third of pronotum, in its wide portion; one very small, smooth, rounded denticle behind them; one comparatively strong, triangular denticle slightly behind the middle. Beyond this rear denticle, the lateral margin of the pronotum is only very indistinctly wavy. Width of anterior margin of pronotum three-fourths its basal width. Pronotum with fine, indistinct shagreening.

142 Elytral shoulders almost one-third wider than pronotal base; sides of pronotal disk smoothly rounded; lateral margin not flat. Elytra more convex than pronotum. Rows of punctures rather distinct, regular; intervals between them broad, flat, finely shagreened. Punctures of rows small, rounded.

Ventrally body uniformly, finely (slightly coarser than dorsally) shagreened.

Dimensions. Body length 1.25 mm.

RHYNCHOPHORA

Beetles belonging to the Rhynchophora were for a long time considered an independent taxon of a high rank; recently, however, they have been assigned

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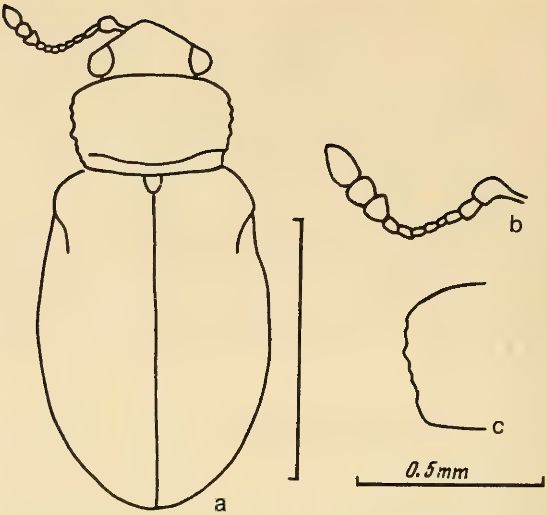
*Given as No. 3311/31 both in Fig. 75 and Plate XII, Photo 4—General Editor.



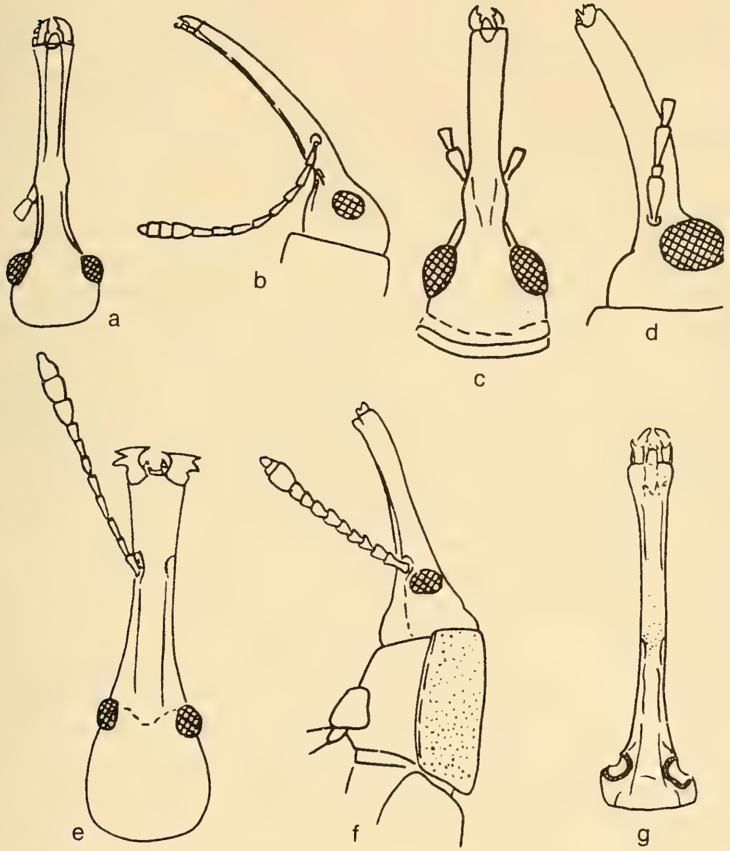
141 Fig. 75. *Succinimontia infleta*, sp. nov.; holotype PIN No. 3311/31: a—dorsal view; b—antenna; c—margin of pronotum. Yantardakh, Upper Cretaceous.

to a superfamily of the infraorder Cucujiformia in which they constitute the most advanced and youngest group. A study of the Mesozoic rhynchophoran material gave a totally unexpected result. In the Late Jurassic, Rhynchophora turned out to be the most diverse and abundant group among all Polyphaga. Moreover, the recent finds of Triassic beetles hardly differing from the Jurassic Eobelidae, compel us to consider them one of the most ancient groups of the Polyphaga. For this reason here we have adopted a neutral position and retained the name Rhynchophora without assigning them a definite rank. Extant Rhynchophora are considered by the author to include 12 families: Belidae, Nemonychidae, Oxycorynidae, Aglycyderidae, Proterrhinidae, Antribidae, Urodontidae, Brenthidae, Attelabidae, Curculionidae, Scolytidae, and Platypodidae.

The exceptionally valuable material on the Late Jurassic insects, collected in the Karatau site of South Kazakhstan, has provided the basis for evaluating the taxonomic position and organizational level of the Late Jurassic Rhynchophora. Like many of the other groups of Coleoptera known from Karatau, the Rhynchophora are already a highly specialized group for which the initial evolutionary stages have long past. They are rich in species and strongly differentiated. However, despite the high level of differentiation, not one of the better preserved specimens examined could be assigned to any of the modern rhynchophoran families, although a few of them exhibit a tendency toward development along some of the same [evolutionary] paths. In these instances it is possible to observe the intial stages of differentiation towards the extant families.

As a preliminary approach to processing the fossil material, the investigator compares it with modern representatives of rhynchophoran families in order to ascertain whether the Mesozoic remains belongs with one of these, or whether it is necessary to erect an independent taxon of familial rank. Naturally, such comparisons should be made with families retaining the most archaic features, such as the Belidae, Nemonychidae and Oxycorynidae (Fig. 76).

The present-day Belidae—inhabiting Australia, South America, and southern North America—possess many indisputably archaic features on top



143 Fig. 76. Head of primitive Rhynchophora; a, b—*Diodirrhynchus austriacus* Oliv., family Nemonychidae, extant; c, d—*Rhinotia* sp., family Belidae, extant; e, f—*Oxycorynus melanocerus* Sc., family Oxycorynidae, extant; g—*Eobelus* sp., family Eobelidae, specimen PIN No. 2384/516; Karatau, Upper Jurassic.

of which they have developed a few specialized characteristics. The Australian genus *Rhinotia* should be considered the most primitive representative among the recent species of this family, since its general appearance is very similar to the Late Jurassic "belidoid" Rhynchophora. However, the whole range of distinguishing features characteristic of Recent Belidae, which are of basic diagnostic importance, differ from those established for Jurassic forms. A low placement of the rostrum is characteristic of all belids; the ventral surface of the rostrum is in line with the gular surface of the head capsule, and the frontal surface of the head capsule forms an angle of up to 90° with the dorsal surface of the rostrum. This type of head structure is peculiar to belids. The pronotum of extant belids has rounded margins, without traces of the notopleural suture or of ridges. The pleurosternal sutures
143 are usually well developed. The antennae of belids lack a club, their first segment is not enlarged, and they are attached at about midlength of the rostrum in males, or at its base in females. The metathorax* is convex, divided by a longitudinal groove. The abdominal sternites are more or less equal in length. The legs are poorly specialized. The mandibles are of the scraping type, with two to three denticles on the broad mesal edge.

A morphological comparison between most Jurassic "belidoid" Rhynchophora and Recent forms shows the usual high degree of similarity in addition to several fundamental differences. The head and rostrum are similar in both groups: the rostrum always originates from the ventral margin of the head capsule in the Jurassic as well as the Recent forms, but the apex of the Jurassic rostrum is broad and noticeably (often strongly) compressed dorsoventrally, whereas in the Recent forms it is cylindrical. The structure of the Jurassic rostrum is very similar to that of primitive Nemonychidae (*Diodirrhynchus*) or Attelabidae (Rhynchitinae). In Jurassic forms the mandibles were apparently always falcate with a single tip, and dorsoventrally flattened as in Nemonychidae. The antennae of all the Jurassic species examined resemble those of Recent Nemonychidae and Rhynchitinae; they are attached in the middle or apical third of the rostrum but never basally. Their first segment is not, or only slightly enlarged in comparison with the following segments; the last three form a loose club. The pronota of all the Late Jurassic "belidoids" have distinct notopleural ridges and probably a corresponding suture or its traces which are absent in Recent belids. The legs
144 of the Jurassic forms are often more specialized than in the extant forms. The abdominal sternites are always of nearly the same length. The comparison thus shows that the Jurassic rhynchophorid beetles cannot be included in the family Belidae.

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*Since the metanotum is covered by the elytra, we may surmise that it is the ventral surface of the metathorax which is indicated here, and presumably the metasternum itself. A ventral perspective can certainly be assumed for the subsequent descriptions of the meso- and metathoraces of fossil rhynchophorans preserved with closed elytra—Scientific Editor.

The Jurassic forms far less strongly resemble the present-day Oxycorynidae. They are similar mainly in having a distinct notopleural ridge. In the present-day oxycorynids the rostrum originates from the middle part of the head capsule and its upper and lower sides form an obtuse angle with the frontal and gular surfaces. In the Oxycorynidae, the antennae are always attached at the base of the rostrum and generally have a rather distinct and compact club which is often four-segmented. None of these characters is known in the Jurassic forms, and consequently the latter cannot be included in the family Oxycorynidae.

There are even fewer common structural features among the Jurassic forms and the extant members of the families Nemonychidae and Attelabidae. These mainly include structural similarities in the apex of the rostrum, in the antennae and to some extent the abdomen. The similarities are least between the Jurassic forms and the extant representatives of the true snout-beetles, family Curculionidae.

Thus, a comparative analysis of the main external morphological features of the fossil Rhynchophora shows that they do not belong to any of the Recent families and represent an independent taxon of the familial rank.

The similarity of the main characters in all the Jurassic rhynchophorid beetles studied by the author (with the exception of the controversial ones) strongly suggests that they are the representatives of a single family and do not belong to any of the Recent families. This conclusion is well supported by the fact that, in a single specimen, characteristics restricted to the Jurassic fauna occur in combination with a series of features which are individually diagnostic of various representatives of the most primitive families which are presently relictual. Hence the Jurassic Rhynchophora described here are considered to be representatives of a now extinct special family Eobelidae, whose several offshoots form independent families.

Family EOBELIDAE L. Arnol'di, Fam. Nov.

Diagnosis. Head rounded or transverse, convex frontally, steeply descending to base of rostrum; rostrum disposed in lower part of head capsule so that lower side of rostrum is in line with gular surface. Antennae without distinct scape; first antennal segment not essentially different from other segements or not more than twice as long as second segment. Antennae usually eleven-segmented, with a loose, often indistinct club, attached at about midlength of rostrum or, rarely, closer to its apex. Eyes always well developed, noticeably shifted anteriorly. Pronotum always with distinct notopleural ridge, abdomen with five similar sternites, evidently somewhat movable. Structure of legs normal for superfamily, sometimes highly specialized.

Description. Small- or medium-sized, elongate, slightly convex beetles, apparently with weakly sclerotized elytra. Head including rostrum, pro-, meso- and metathorax as well as extremities highly sclerotized.

Head capsule laterally rounded, generally transverse, occipital foramen wide. Eyes always well developed, not placed laterally but noticeably shifted forward toward the frontal part of capsule, small or moderately large, rounded. Frontal surface convex, generally projecting anteriorly and dorsally. Rostrum for the most part rather slender, always well developed, located on lower part of head capsule, its lower side in line with gular surface, upper 145 side forming right angle or obtuse angle (90–130°) with frontal surface. Length of rostrum highly variable, never less than the length of pronotum. It [= rostrum] is straight or curved to a varying degree, curvature usually very gentle. In most cases, rostrum flattened toward apex and broadened to a varying degree, as in Nemonychidae (*Diodirrhynchus*) or Rhynchitinae. The structure of mouth parts could not be studied in the usual detail, but in some impressions their structure was rather close to the extant Nemonychidae (*Diodirrhynchus*), i.e., mandibles with a singe apex and flattened dorsoventrally, without large denticles. Maxillae apparently free, not covered by mentum and with highly reduced palps. Distinct gular sutures visible in good impressions. Antennae generally attached near midlength of rostrum, rarely close to its apex, and never at its base. A short, shallow pit is sometimes noticeable at the place of antennal attachment and may represent a rudiment of the future antennal socket. Antennae attached at the base of rostrum in a single specimen, thick and strongly broadening toward apex, displaying features of considerable specialization. In the same specimen, mandibles also considerably enlarged, resembling those in males of some Recent Brentidae. In all specimens in which antennae are well preserved, they are eleven-segmented, with a loose, poorly differentiated three-segmented, club; none with a marked elongation of the first segment, at most 1.5 to 2 times longer than the following segments; second or third segment sometimes elongate, i.e., the Jurassic forms still lacked the present-day scape and their antennae were not geniculate.

Viewed laterally, prothorax always shows distinct division into notal and sternal parts; notopleural ridge distinctly visible. A notopleural suture, sometimes noticeable below the ridge, apparently also present. The sculpturing on pronotum usually coarser than on pleura, with dense and rather coarse punctation. Shape of pronotum rather uniform, generally transverse, weakly rounded laterally, anteriorly weakly emarginate, basally straight or weakly emarginate. Forecoxae always set part, generally by less than half their diameter.

Elytra usually elongate, more or less parallel-sided, rarely uniformly and weakly rounded. Elytra rarely short and broad. Punctate grooves, rows of punctures or pits generally distinct. No hairs, scales or bristles visible, although they would have been visible [if present] on several of the high quality impressions. Apices of elytra jointly or rarely separately rounded. In one specimen each apex extended into a short triangular cusp. Lateral (epipleural) margin of elytra usually slightly curved above hind coxae or almost straight.

In most cases the mesothorax could not be examined in detail, nevertheless all its sutures were definitely present and the sclerites were differentiated. Scutellum very rarely visible; middle coxae generally separated by a distance nearly equal to their diameter, sometimes wider. Metasternum well developed in all but one example, long usually 2.5–3 times longer than diameter or coxae; episterna rectangular, sometimes with longitudinal suture or groove.

Abdomen always with five similar sternites, more or less movable. Signs of fusion between the first and second sternites or of a pronounced enlargement of the first sternite were not observed.

Structure of legs differs little from that in Recent families. In more primitive forms, they have slightly dialated straight femora, slender straight tibiae, and long narrow tarsi. In a number of cases, first [tarsal] segment largest and broadest, third always bilobed, unguiculate segment narrow and moderately long. In some Jurassic forms, the legs display highly specialized features: femora strongly thickened, particularly the forefemora which are sometimes thicker than long; tibiae slender, straight and short; tarsi excep-
146 tionally enlarged, almost equal in length to tibiae, but more than three times the width of tibial apex, apparently covered by dense and soft setae since their margins are highly diffuse in the impressions. There is evidence to indicate that such tarsi are a secondary sexual character of males. In others with normal femora, strongly curved tibiae or tibiae armed with apical spurs are present.

Composition. Four subfamilies in the Late Jurassic of South Kazakhstan, described below.

Comparison. Resembles Belidae in the position of rostrum, the lower side of which is continuous with the ventral surface of head, but differs from it in the ridge and traces of a suture on the sides of pronotum, dorsoventral flattening of the apex of rostrum and the frequently clavate antennae. Resembles Oxycorynidae in the structure of prothorax; resembles Nemonychidae and Attelabidae (Rhynchitinae) in the structure of antennae and apex of rostrum, but differs from them in the character of rostral base.

Remarks. The study of often incomplete and inadequately distinct impressions of insects poses considerable difficulties in the taxonomic treatment of the Mesozoic material. The impossibility of utilizing the whole range of characters encountered in the extant forms, frequently impels one to study only the most noticeable external features, making the conclusions less reliable and occasionally tentative. The nature of the fossilization and subsequent deformation of the impressions under heavy pressure, hinders identification of a specimen's species or genus; it is [therefore] possible that specimens of a single species will be described under different genera. Despite these difficulties, an experienced taxonomist usually finds significant distinguishing characters to build a phylogenetically based system of classification.

Subfamily Eobelinae L. Arnol'di Subfam. Nov.

Diagnosis. Rostrum generally slender and long, usually longer than head capsule and pronotum together. Antennae attached at middle of rostrum or near it. Pronotum small, dorsally flat, lateral ridges not sharp. Elytra usually more or less parallel-sided or with a weakly rounded lateral margin, dorsally flat or weakly convex. Abdomen with fairly similar sternites. Legs often highly specialized, with distinctly thickened femora and enlarged tarsi. Hind tibiae sometimes with large apical spur.

Composition. Three tribes in the Late Jurassic of South Kazakhstan.

Comparison. Most closely resembles the subfamily Oxycorynoidinae, differs in the absence of sharp ridges on the sides of pronotum and usually longer and thinner rostrum.

Tribe EOBELINI L. Arnol'di, trib. nov.

Diagnosis. Rostrum slender and long, considerably longer than head capsule and pronotum together, almost straight or very slightly curved. Elytra flat or weakly convex, more or less parallel-sided, epipleural margin slightly curving above hind coxae. Legs with slender straight femora and tibiae, or specialized with highly thickened forefemora and very large foretarsi, or with hind tibiae armed with large spurs.

Composition. Five genera in the Late Jurassic of South Kazakhstan (Karatau).

Comparison. Distinguished from other tribes by the longer rostrum.

147 Genus *Eobelus* L. Arnol'di, gen. nov.

Type species. E. longipes, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Most strongly resembles present-day Belidae in general appearance. Head strongly convex in frontal part, with large eyes. Rostrum long, almost cylindrical, slightly curved. Pronotum flat, with notopleural ridge. Elytra more or less parallel-sided, flat. Legs long, with slender femora slightly thickened toward middle, tibiae slender and straight, tarsi long and narrow. Metathorax moderately convex.

Species composition. Monotypic genus.

Comparison. Differs from other species in almost not thickened forefemora and flat elytra.

Remarks. Based on general appearance, structure of legs, elytra and head, this genus is apparently the most primitive of all the Jurassic Rhynchophora studied by the author.

Eobelus longipes L. Arnol'di, sp. nov.

(Plate XII, Photo 5; Figure 77)

Species name coined from 'longipes' (Latin)—long-legged.

Holotype. No. 2452/275, PIN, almost entire impression of a beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley near Uspenskoe (Karatau-Galkino site). Upper Jurassic, Karabastau series.

Material. Besides holotype, impression of a beetle lying on its back, specimen No. 2384/516 from Karatau-Mikhailovka site (Fig. 76g) possibly belonging to this species.

Description. Head rather larger, convex, frontal part sloping to base of rostrum at an angle of about 80°. Eyes large, round, their lower margin not reaching lower side of rostrum by about one-third the width of rostral base, their length almost one-and-a-half times that of latter. Rostrum very slightly curved, noticeably thin in apical third. Antennae noticeably shorter than rostrum, with comparatively distinct club. Pronotum dorsally flat, distinctly and rather prominently punctate on disk. Prothorax with pleurosternal suture. Elytra weakly convex, apices acutely angled, 3.3 times longer than pronotum, rather fine punctures visible on anterior half of disk. Metathorax long, but comparatively weakly convex. Forelegs with almost nonclavate long femora, longer than pronotum; tibiae even longer, narrow and almost straight, 1.75
148 times longer than rostrum. Foretarsi narrow. Middle femora shorter and thinner than forefemora, tibiae straight and slender, hind femora not thinner than middle and of same length, tibiae straight, tarsi slender and long. Third bilobed tarsal segment small, shorter than remaining segments.

Dimensions. Body length 8.2 mm (here and throughout the remainder of the text the body length does not include the rostrum); length of rostrum 3.6 mm.

Genus *Archaeorrhynchus* Martynov, 1926

Type species. A. tenuicornis Martynov, 1926; Upper Jurassic of South Kazakhstan.

Diagnosis. Rostrum almost straight, noticeably thinning toward apex, dorsoventrally flat at apex. Antennae with slightly elongate first three segments. Sides of pronotum with notopleural ridge. Forefemora strongly thick-

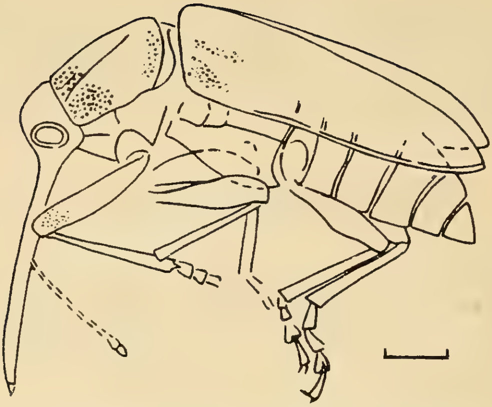


Fig. 77. *Eobelus longipes*, sp. nov.; holotype PIN No. 2452/275. Karatau, Upper Jurassic.

ened, sometimes thicker than height of head capsule, foretarsi generally very large (in males ?) and wide, particularly their first segment. Metathorax convex.

Species composition. Four species in the Late Jurassic of South Kazakhstan.

Comparison. Differs from all genera except *Probelus* in the strongly thickened femora, differs from the latter in the straight foretibiae.

Remarks. The genus *Archaeorrhynchus* was established by Martynov (1926) from the same Karatau site. The detailed description and good illustration leave no doubt that Martynov described a representative of the same genus as that which was present in the material examined by me. However, Martynov's description indicates the presence of a fine and long shaft (scape) and an antennal groove in his *A. tenuicornis* Mart. This feature was not observed in any of the well preserved antennae in the material at my disposal. Even markedly elongate first segments have never been observed, and it is definite that geniculate antennae did not yet exist in the Jurassic forms, rather Martynov mistook the distinct impression of the flagellum for the scape, and the two lateral margins of the basal part of the rostrum for the antennal grooves.

Archaeorrhynchus acutirostris L. Arnol'di, sp. nov.
(Figure 78)

Species name coined from 'acutis' (Latin)—sharp, and 'rostrum' (Latin)—beak.

Holotype. No. 2554/715, PIN, almost entire impression of a beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head rather large, with frontal surface steeply descending from temple to rostrum, forming almost right angle. Eyes comparatively small, round. Rostrum rather slender, basally thinner than length of eyes, markedly thinning toward apex, almost subulate (in lateral position !), in apical half slightly curving from point of antennal attachment. Antennae attached almost at middle of rostrum, their structural details indistinct in basal half, but undoubtedly lacking a long scape; club weakly differentiated. Lower side of rostrum slightly convex from base, as a result a slight gular indentation is observed. Pronotum transverse with basal arcuate emargination. Elytra apparently elongate-oval, their apical angles acute, faint grooves discernible on disk, lateral margins almost straight. Metathorax rather convex, [ventrally] almost twice as long as width of hind coxae. Abdomen with subequal 149 sternites, third being the shortest. Specimen apparently female since abdomen extends posteriorly into a short tube. Forelegs considerably larger than others, their femora strongly thickened, tibiae slender, tarsi not preserved. Middle femora approximately half the thickness of forefemora, tibiae straight, tarsi large and long. Hind legs shorter than others, hind femora somewhat thicker than middle femora and two-thirds their length; tibiae straight, tarsi comparatively small.

Dimensions. Body length 7.8 mm, length of rostrum 3.2 mm.

Comparison. Distinguished by hind femora which are much shorter than middle femora.

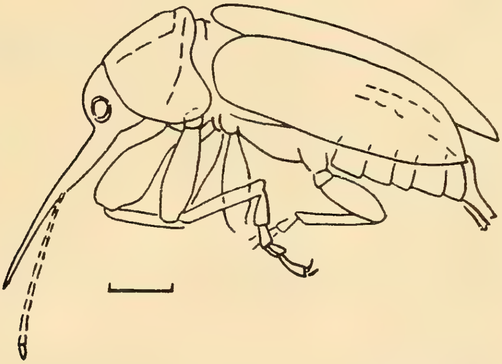


Fig. 78. *Archaeorrhynchus acutirostris*, sp. nov.; holotype PIN No. 2554/715. Karatau, Upper Jurassic.

Archaeorrhynchus paradoxopus L. Arnol'di, sp. nov.
(Plate XII, Photo 6; Figure 79)

Species name coined from 'paradoxa' (Greek)—strange, and 'pous' (Greek)—foot.

Holotype. No. 2335/42, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kash-karata river valley, Uspenskoe settlement (Karatau-Galkino site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head moderately large, short; frontal surface forming an almost right angle with rostral base. Eyes moderately large, longitudinally slightly oval, shifted anteriorly. Rostrum long, basally narrower than length of eyes, strongly thinning distally, subulate, almost straight. Antennae attached in basal half of rostrum, their first segment longer than remaining segments, club present but poorly differentiated. Total antennal length almost equal to length of rostrum. Pronotum dorsally flat; length of rostrum 2.3 times greater than pronotal length along upper surface. Punctation fine, dense. Elytra slightly convex, posteriorly abruptly rounded off, rows of large punctures distinctly visible on disk. Length of elytra three times that of pronotum. Epipleural margin straight. Prothorax small, forecoxae shifted 150 closer to its posterior margin. Metathorax long, more than three times longer than width of hind coxae, moderately convex, metepisterna broad, fine transversely rugose punctation distinctly visible. Abdomen with similar sternites, apically rounded. Forelegs with very strongly thickened femora, femoral thickness three times that of rostral base. Foretibiae comparatively slender and straight. Tarsi very large, almost as long as tibiae and more than two-and-a-half times wider than them. Their structural details could not be examined; apparently they are densely covered by fine pubescence, and are structurally similar to the tarsi of *A. acutirostris*, sp. nov. Middle femora weakly clavate, with fine transverse striations; tibiae long and straight; tarsi slender. Hind femora thinner and shorter; tibiae straight, short, apically apparently with tuft of bristles; tarsi slender.

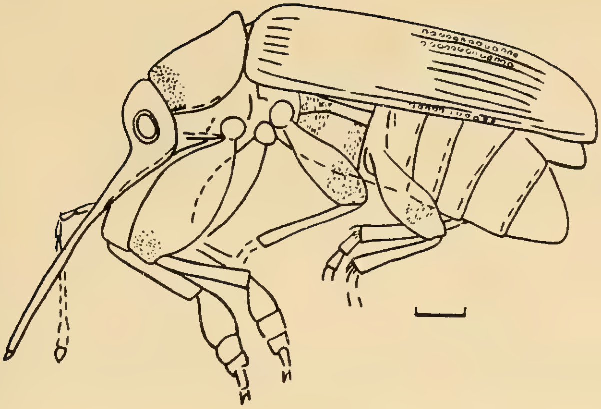
Dimensions. Body length 10.2 mm, length of rostrum 5.4 mm.

Comparison. Resembles *A. latitarsus* in the structure of foretarsi, differs from it in smaller head.

Archaeorrhynchus latitarsus L. Arnol'di, sp. nov.
(Figure 80)

Species name coined from 'latus' (Latin)—wide, and 'tarsus' (Latin)—foot.

Holotype. No. 2239/531, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kash-



149 Fig. 79. *Archaeorrhynchus paradoxopus*, sp. nov.; holotype PIN No. 2335/42. Karatau, Upper Jurassic.

karata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head massive, frontal surface rather steeply descending to base of rostrum, forming an angle of about 50° with its upper surface. Eyes round, small, their lower margin level with upper side of rostrum. The latter relatively thick, more than length of eyes, uniformly narrowing toward apex and very slightly curved. Antennae attached at end of basal third of rostrum, slender, with non-abrupt club. First antennal segment longest; second approximately one-third and third only slightly shorter than first, following

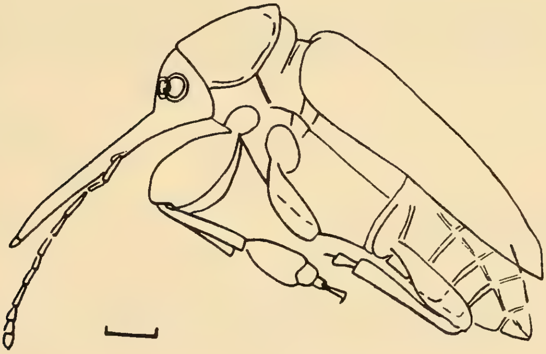


Fig. 80. *Archaeorrhynchus latitarsus*, sp. nov.; holotype PIN No. 2239/531. Karatau, Upper Jurassic.

segments less than half of third. Total antennal length almost equal to that of head including rostrum, segments of club triangular, last segment rhomboidal. Pronotum short, posteriorly rounded, with distinct notopleural ridge, dorsally weakly convex. Elytra apparently more or less parallel-sided, angularly tapering apically. Epipleural margin of elytra straight. Prothorax rather high [= tall], forecoxae closer to its posterior margin. Mesothorax short, with distinct sutures between sclerites, middle coxae large. Metathorax very long, 3 times longer than width of hind coxae, uniformly convex, epimera rectangular. Abdomen with similar segments, longer than elytra. Forelegs with 151 strongly thickened femora, their width 3 times the basal thickness of rostrum. Foretibiae rather slender, almost straight; tarsi strongly dialated, their first segment two-and-a-half times broader than tibial apex, apically emarginate; second segment anteriorly tapering, one-third the length of first; third very small; unguiculate segment short and apparently slender. Middle femora slightly thickened. Hind legs with gently clavate femora; slender, straight tibiae, and slender tarsi.

Dimensions. Body length 8.8 mm, length of rostrum 3.8 mm.

Comparison. Differs from closely related *A. paradoxopus* in the more massive head, and sloping frons.

Genus *Probelus* L. Arnol'di, gen. nov.

Genus name coined from genus *Belus.*

Type species. P. curvispinus, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Head large or moderately large; rostrum almost straight, longer than head capsule and pronotum together. Antennae slender, with distinct club, slightly shorter than rostrum, attached before its middle. Pronotum short, transverse, with sharp notopleural ridge, dorsally flat. Elytra more or less parallel-sided, dorsally flat. Foremora slightly or moderately clavate, tibiae slightly curved, tarsi small or long, but narrow. Hind tibiae having mild preapical depression on inner side, with large straight or arched spur on anterior apical angle.

Species composition. Three species in the Late Jurassic of South Kazakhstan.

Comparison. Differs from other genera in hind tibiae with depression on inner side and large apical spur.

Probelus curvispinus L. Arnol'di, sp. nov.
(Plate XIII, Photo 1; Figure 81)

Species name coined from 'curvus' (Latin)—curved, and 'spina' (Latin)—point, spur.

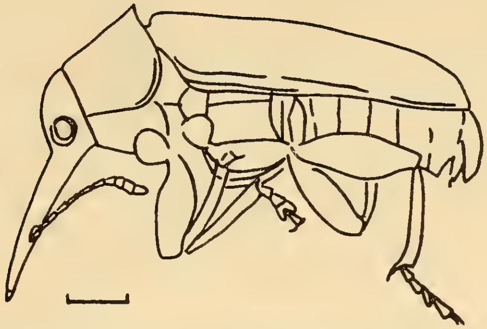


Fig. 81. *Probelus curvispinus*, sp. nov.; holotype PIN No. 2554/709. Karatau, Upper Jurassic.

Holotype. No. 2554/709, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head moderately large, frontally convex, forming right angle with base of rostrum. Eyes small, somewhat larger than basal width of rostrum, rounded; rostrum almost straight, strongly tapering toward apex; antennae attached at beginning of anterior third of rostrum, their first segment not enlarged. Pronotum with weakly raised posterior margin. Elytra almost flat, 3.3 times longer than pronotum, epipleural margin scarcely curved. Legs short, all femora rather strongly clavate, particularly forefemora. All tibiae curved; fore and middle tibiae short; hind tibiae longer, depressed preapical-
152 ly, apical angle extending into falcate spur, directed anteriorly and ventrally. Foretarsi small, structure typical, hind tarsi narrow but apparently long.

Dimensions. Body length 7.0 mm, length of rostrum 3.2 mm.

Comparison. Differs from other species in more strongly thickened femora.

Probelus longitarsus L. Arnol'di, sp. nov.
(Figure 82)

Species name coined from 'longus' (Latin)—long, and 'tarsus' (Latin)—foot.

Holotype. No. 2066/2811, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

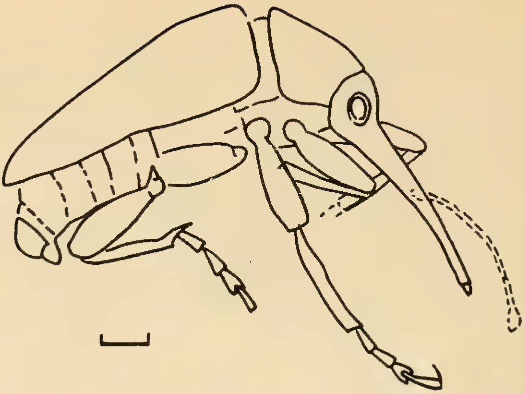


Fig. 82. *Probelus longitarsus*, sp. nov.; holotype PIN No. 2066/2811. Karatau, Upper Jurassic.

Material. Holotype.

Description. Head small, frontal surface forming angle of about 100° with upper side of rostrum. Eyes small, their lower margin almost level with upper side of rostrum. The latter slender, moderately tapering toward apex, somewhat more noticeably curved preapically, its length 1.3 times that of head capsule and pronotum together. Antennae attached immediately before rostral middle, slender and rather long, their details indistinct. Pronotum very slightly convex dorsally, its posterior margin slightly upcurved. Elytra weakly convex, acute angled apically, epipleural margin slightly emarginate above hind coxae. Metathorax long, [ventrally] convex. Legs with moderately thickened femora, middle tibiae noticeably curved in basal fourth, and smoothly depressed preapically on inner side. Hind tibiae weakly curved anteriorly, with broad and gently sloping preapical depression on inner side, apical spur short, curved. Foretarsi poorly preserved, but undoubtedly narrow; middle and hind tarsi narrow and long, only slightly shorter than tibiae.

Dimensions. Body length 8.0 mm, length of rostrum 3.2 mm.

Comparison. Differs from type species in possessing less thickened femora, from *P. tibialis* in curved spurs of hind tibiae.

Probelus tibialis L. Arnol'di, sp. nov.

(Figure 83)

Species name coined from 'tibia' (Latin)—shin.

Holotype. No. 965/45, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Uspenskoe settlement (Karatau-Galkino site). Upper Jurassic, Karabastau series.

153 *Material.* Holotype.

Description. Head large, transverse; eyes large, strongly shifted forward. Rostrum rather wide, with distinct though slight constriction at juncture with antennae, i.e., apex of rostrum slightly broad at commencement of apical third. Antennae rather short, third segment longest, club distinct. Pronotum anteriorly weakly emarginate, almost straight basally, sides moderately rounded. Elytra longitudinally oval, parallel-sided in anterior half. Forecoxae strongly convergent, not contiguous, middle coxae also slightly separated, hind coxae separated by half their length. Meso- and metathorax [ventrally] with longitudinal groove. Length of metathorax twice the width of hind coxae. Legs with slightly clavate femora and rather thick, very slightly curved tibiae; hind tibiae notched, apex of spur straight; tarsi slender and short.

Dimensions. Body length 7.3 mm, width 2.6 mm; length of rostrum 1.9 mm.

Comparison. Differs from type species in possessing slightly [as apposed to greatly] thickened femora, and from *P. longitarsus* in straight spurs of hind tibiae.

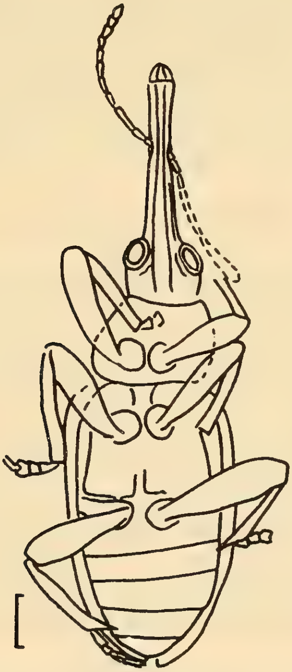


Fig. 83. *Probelus tibialis*, sp. nov.; holotype PIN No. 965/45; Karatau, Upper Jurassic.

Remarks. This species is included in the genus *Probelus* on the basis of the structure of the hind tibiae and general proportions of the body. Comparison with other species is not possible since the fossil is positioned on its back.

Genus *Probelopsis* L. Arnol'di, gen. nov.

Genus name coined from genus *Belus.*

Type species. P. acutiapex, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Head small; rostrum almost straight, slightly curved only in apical third. Eyes large, their width 1.4 times the basal width of rostrum. Elytra flat, apparently parallel-sided, their apices weakly drawn out into short triangular processes. Legs with moderately clavate femora, forefemora slightly thicker than remaining femora, tibiae rather slender, fore- and middle tibiae slightly curved, hind tibiae straight. Inner angles of fore- and hind tibiae with short spurs.

Species composition. Monotypic genus.

154 *Comparison.* Differs from the preceding two genera in the less thickened femora, differs slightly from the first* in the drawn out elytral apices, and from the remaining genera in the almost straight rostrum.

Probelopsis acutiapex L. Arnol'di, sp. nov.
(Plate XIII, Photo 2; Figure 84)

Species name coined from 'acutus' (Latin)—pointed, and 'apex' (Latin)—tip.

Holotype. No. 2239/1554, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head not high**, eyes large, round, rostrum long. Antennae attached at two-fifths the length of rostrum from base. Rostrum longer than head capsule and pronotum together. Pronotum rather short, dorsally noticeably convex, notopleural ridge distinct, forecoxae at posterior margin of prothorax. Elytra slightly convex dorsally, anteriorly truncate, weakly emarginate on epipleural margin. Elytral apices drawn out into short points. Legs rather long, femora very weakly clavate, forefemora thicker, their

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*In this context the term 'first' probably refers to the genus *Eobelus* which is the first genus listed in the tribe Eobelini—Scientific Editor.

**As used here, the term 'high' does not refer to the orientation or position of the head, but to the length of its dorsoventral axis—Scientific Editor.

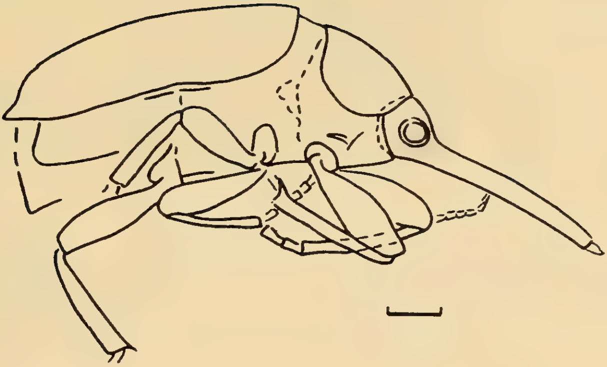

Fig. 84. *Probelopsis acutiapex*, sp. nov.; holotype PIN No. 2239/1554; Karatau, Upper Jurassic.

thickness almost twice the basal width of rostrum. Foretibiae linear up to apical fourth and here noticeably curved, middle tibiae weakly and uniformly curved, hind tibiae almost straight. Spurs on fore- and hind tibiae resemble a short spine, directed anteriorly. Tarsi almost not preserved, but were apparently slender and short.

Dimensions. Body length 7.3 mm, length of rostrum 2.8 mm.

Genus *Belonotaris* L. Arnol'di, gen. nov.

Genus name coined from genera *Belus* and *Notaris.*

Type species. B. punctatissimus, sp. nov.; Upper Jurassic of South Kazakhstan.

Diagnosis. Head small, rostrum long, always uniformly and smoothly curved; antennae attached at middle. Elytra noticeably convex, usually with rows of punctures, with distinct emargination of epipleural margin above hind coxae. Legs with slightly thickened femora, tibiae lacking armature, and small tarsi.

Species composition. Three species (one included tentatively) in the Jurassic of South Kazakhstan.

Comparison. Distinguished by convex elytra with distinct emargination of epipleural margin, uniformly curved rostrum and tibiae lacking armature.

155 *Belonotaris punctatissimus* L. Arnol'di, sp. nov.
(Plate XIII, Photo 3; Figure 85)

Species name coined from 'punctum' (Latin)—point.

Holotype. No. 2452/422, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Karabastau area (Karatau-Karabastau site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head small, frontal surface smoothly descending to base of rostrum, forming obtuse angle (about 120-130°) with it. Eyes small, round. Rostrum slender, long, smoothly curved, its length somewhat more than total length of head capsule plus pronotum. First three segments of antennae small, cylindrical. Pronotum rather long, dorsally weakly convex, with dense and coarse punctation. Elytra elongate, moderately convex, with rather strongly curved epipleural margin, with distinct rows of large punctures, probably forming a honeycombed pattern. Metathorax weakly convex, abdomen with similar sternites. All femora moderately clavate, 1.7 times thicker than base of rostrum; tibiae poorly preserved, but apparently straight and comparatively slender; tarsi not preserved.

Dimensions. Body length 6.2 mm, length of rostrum 2.2 mm.

Comparison. Distinguished by longer pronotum.

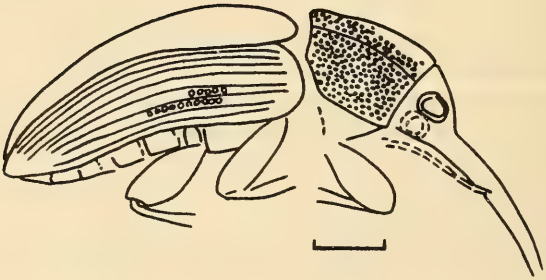

Fig. 85. *Belonotaris punctatissimus*, sp. nov.; holotype PIN No. 2462/422*; Karatau, Upper Jurassic.

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*Given as 2452/422 in the Text and Plate XIII—General Editor.

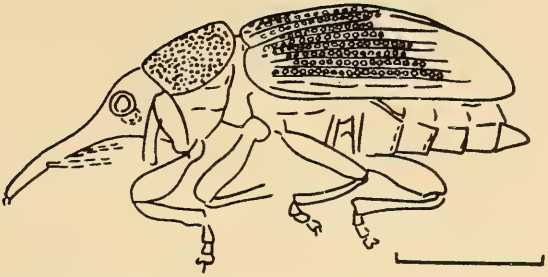


Fig. 86. *Belonotaris lineatipunctatus*, sp. nov.; holotype PIN No. 2066/3209; Karatau, Upper Jurassic.

Belonotaris lineatipunctatus L. Arnol'di, sp. nov.
(Figure 86)

Species name coined from 'linea' (Latin)—line, and 'punctum' (Latin)—point.

Holotype. No. 2066/3209, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head small, frontal surface sloping to form obtuse angle of 120–30° with upper side of rostrum; eyes round, their diameter 1.2 times the 156 basal width of rostrum. Rostrum slender, uniformly weakly curved, its length somewhat less than total length of head capsule and pronotum. Antennae attached at about middle of rostrum, somewhat closer to its apex. They were poorly preserved but definitely without a distinctly elongate first segment. Pronotum short, weakly convex, dorsally with fine and dense punctation; elytra noticeably convex, with punctate grooves, punctures in them large, forming a honeycomb pattern. Lateral margins of elytra strongly curved (possibly as a result of distortion of the specimen during fossilization). Abdomen with identical sternites, posteriorly pointed. Legs rather slender and long, forefemora more strongly clavate than remaining femora. Tibiae almost straight, tarsi small and slender.

Dimensions. Body length 2.9 mm, length of rostrum 1.2 mm.

Comparison. Distinguished by short pronotum.

Belonotaris karatavicus L. Arnol'di, sp. nov.
(Figure 87)

Species named after Karatau.

Holotype. No. 2066/2552, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head small, frontal surface initially more gently sloping, then sharply descending almost at right angles to base of rostrum. Eyes round, rather large, slightly larger than basal width of rostrum. The latter long, 2.25 times longer than pronotum, moderately thick, weakly and uniformly curved, gradually thinning toward apex. Antennae attached just anterior to middle, slender, with distinct three-segmented club; antennal length somewhat less than that of rostrum. Pronotum a little convex, twice as long as head capsule. Elytra moderately and uniformly convex, apices of angles acute, epipleural margin noticeably emarginate above hind coxae. Metathorax comparatively short, less than twice as long as width of hind coxae. Abdomen considerably projecting beyond elytral apex. Legs with weakly clavate femora; tibiae slightly curved, slender; tarsi poorly distinguishable but undoubtedly small.

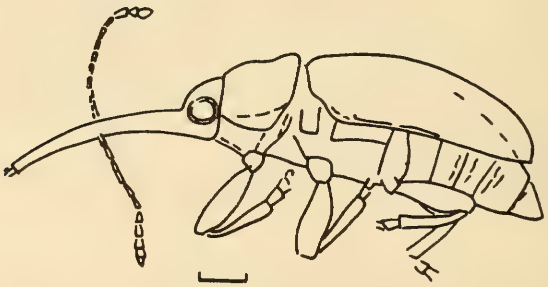
Dimensions. Body length 8.5 mm, length of rostrum 4.0 mm.

Comparison. Differs from other species in the shape of head whose frontal surface forms almost right angle with rostrum.

Remarks. Inclusion of this species in the genus *Belonotaris* raises some doubts since the body proportions do not fully coincide with those of the two preceding species. However, the shape of rostrum and elytra, and also the structure of legs are very similar to those in the aforementioned species.

157 Tribe PROCURCULIONINI L. Arnol’di, trib. nov.

Diagnosis. Rostrum long, thick, distinctly narrowing at antennal junction, apical part somewhat broadened. Mandibles large. Length of pronotum



156 Fig. 87. *Belonotaris karatavicus*, sp. nov.; holotype PIN No. 2066/2552; Karatau, Upper Jurassic.

exceeding its width by less than two times, apical margin projecting at middle. Elytra parallel-sided. Forefemora thickened.

Composition. Single genus in the Late Jurassic of South Kazakhstan.

Comparison. Differs from Eobelini in short thick rostrum, and elytra without emargination of lateral margin; from Eccoptothoracini in the longer pronotum.

Genus *Procurculio* L. Arnol'di, gen. nov.

Genus name coined from genus *Curculio*.

Type species. P. fortipes, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Rostrum narrowest at beginning of anterior third, its preapical part broad, parallel-sided. Mandibles almost as long as apical width of rostrum. Pronotum strongly rounded laterally, its anterior margin very slightly projecting at middle.

Species composition. Monotypic genus.

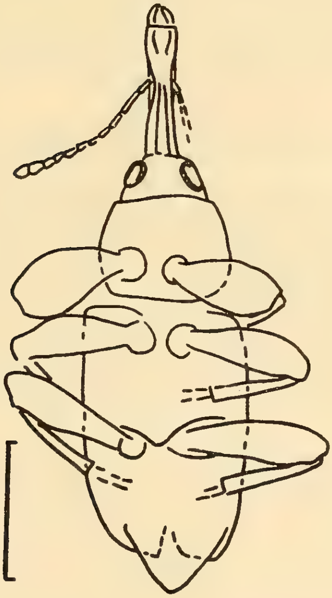


Fig. 88. *Procurculio fortipes*, sp. nov.; holotype PIN No. 2066/2339; Karatau, Upper Jurassic.

Procurculio fortipes L. Arnol'di, sp. nov.
(Plate XIII, Photo 4; Figure 88)

Species name coined from 'fortis' (Latin)—strong, and 'pes' (Latin)—foot.

Holotype. No. 2066/2339, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head capsule almost semicircular, frontally steeply descending to base of rostrum, which is somewhat shorter than head capsule and pronotum together, gradually narrowing up to anterior third where antennae are attached, then broadening sharply for a short distance, but further on up to apex again parallel-sided. Base of rostrum only slightly narrower than the interorbital width of frons. Antennae slender, their second and third segments longer than remaining segments, club not abrupt; antennal length equal to rostrum and head capsule together. Pronotum transverse, laterally rounded, maximum width behind middle, appreciably narrower at posterior margin than at anterior. Elytra 2.5 times longer than pronotum and only 1.2 times broader, parallel-sided up to apical third, apices together broadly rounded. Metathorax long; abdomen somewhat protruding beyond elytral apices. Legs long; forefemora shorter than others, strongly swollen; middle and hind femora slightly thickened, almost straight; tarsi apparently narrow.

Dimensions. Body length 7.5 mm, length of rostrum 2.4 mm.

158 Tribe ECCOPTOTHORACINI L. Arnol'di, trib. nov.

Diagnosis. Rostrum rather short, moderately thick. Pronotum strongly transverse, its length less than half its width at base, posterior angles acute. Anterior margin smoothly emarginate, emarginate basally [too]. Abdomen with first three sternites identical, fourth considerably narrower with strongly rounded emargination at posterior margin, fifth blunt. Legs not thickened.

Composition. Single genus in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished by strongly transverse pronotum, tapering anteriorly.

Genus *Eccoptothorax* L. Arnol'di, gen. nov.

Genus name coined from 'eccopte' (Greek)—emarginate, and 'thorax' (Greek)—chest.

Types species. E. latipennis, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Rostrum tapering from base to place of antennal attachment slightly anterior to its middle. Length of pronotum two-fifths its basal width, anterior margin noticeably narrower than posterior, latter deeply emarginate. Metathorax long.

Species composition. Monotypic genus.

Eccoptothorax latipennis L. Arnol'di, sp. nov.
(Plate XIII, Photo 5; Figure 89)

Species name coined from 'latus' (Latin)—broad, and 'penna' (Latin)—wing.

Holotype. No. 2554/720, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head short and wide, rostrum moderately long, longer than head capsule and pronotum together, moderately thick, apical part broader

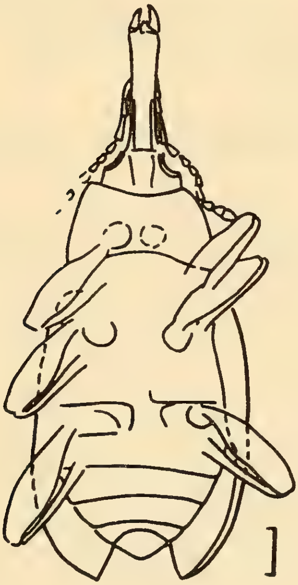


Fig. 89. *Eccoptothorax latipennis*, sp. nov.; holotype PIN No. 2554/720; Karatau, Upper Jurassic.

than base. Antennae rather long, not shorter than head with rostrum. Their first four segments slightly larger than remaining segments, club distinct. Mandibles rather long. Pronotum laterally broadened from anterior to posterior margin, both margins noticeably emarginate. Abdomen atypical of Jurassic Rhynchophora: its sternites gradually decreasing in size from first to fourth, which is strongly rounded and emarginate at posterior margin, while the fifth set into the notch of fourth by almost half its length, posteriorly triangular. Elytra rather wide, almost parallel-sided, probably convex in posterior half. Broad, turned-under elytral epipleura may be the result of flattening. Femora weakly clavate, rather long; tibiae poorly visible, but apparently not thick, slightly curved or straight. Tarsi not visible.

Dimensions. Body length 6.5 mm, length of rostrum 1.8 mm, elytral width in anterior half 2.6 mm.

159 **Subfamily Oxycorynoidinae L. Arnol'di, Subfam. Nov.**

Diagnosis. In general appearance very closely resembles Oxycorynidae. Rostrum moderately long, antennae attached at its middle. Pronotum with sharp longitudinal lateral ridge. Abdomen with rather similar sternites. Legs usually rather short, sometimes with tibiae distinctly curved or armed with short spurs.

Composition. Three tribes in the Late Jurassic of South Kazakhstan.

Composition. Resembles subfamily Eobelinae, differs in distinct longitudinal ridge of prothorax.

Tribe OXYCORYNOIDINI L. Arnol'di, trib. nov.

Diagnosis. Small or minute compact beetles; in most cases [length of rostrum]* not exceeding the length of head capsule and pronotum together, rarely somewhat longer. Rostrum usually nearly straight, more rarely moderately curved, usually slightly broadening at apex. Antennae always attached near rostral middle. Position of rostrum on head capsule typical of belidoids, but sometimes (if not owing to distortion during fossilization) on the lower side, not fully in line with the gular surface. Elytra weakly convex or flat, rounded or pointed apically, with acute sutural angle. Abdomen with rather similar sternites. Legs usually small, generally lacking specialized features; tibiae sometimes curved or armed with small spurs.

Composition. Four genera in the Late Jurassic of South Kazakhstan, of which two (*Ampliceps* and *Paroxycorynoides*) stand somewhat apart and probably merit separation into independent taxa of tribal rank. However, the data are insufficient for such a separation, and hence they are included in this tribe.

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*The bracketed part of this phrase was extrapolated from the context; it was apparently accidentally omitted in the Russian original—Scientific Editor.

Comparison. Distinguished from other tribes by the normal structure of legs and antennal attachment close to midrostrum.

Genus *Oxycorynoides* L. Arnol'di, gen. nov.

Genus name coined from genus *Oxycorynus.*

Type species. O. similis, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Comparatively short, compact, minute beetles. Head moderate sized, rarely large, high*; eyes round, generally small. Length of rostrum somewhat less than combined length of head capsule and pronotum, rarely slightly more; rostrum straight or slightly curved, slightly tapering toward apex (appears to be broadening apically in lateral, dorsal or ventral views), antennae generally attached somewhat anterior to its middle. Pronotum short, weakly transverse, with posterior angles rounded, notopleural ridge present. Elytra weakly convex, apically with acute sutural angle or more rarely rounded. Legs usually short, lacking specialized features, tibiae straight, tarsi always slender, small.

Species composition. Six species (one tentatively included in this genus) in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished by slightly thickened femora and straight tibiae.

Oxycorynoides similis L. Arnol'di, sp. nov.
(Plate XIII, Photo 6; Figure 90)

Species name coined from 'similis' (Latin)—similar.

Holotype. No. 2554/713, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kash-160 karata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head moderately large; eyes slightly less than half the height of head capsule at pronotal margin, round, positioned against rostral base. Frontal surface forming obtuse angle (about 130°) with base of rostrum, gular surface not coplanar with lower side of rostrum, forming an angle of about 140–150° with it. Length of rostrum somewhat less than combined length of head capsule and pronotum. Rostrum almost straight, slightly thinning toward apex, antennae attached at its midlength. Pronotum weakly convex, short. Elytra weakly convex in posterior half, with acute apical angle.

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*See our comment on page 208—Scientific Editor.

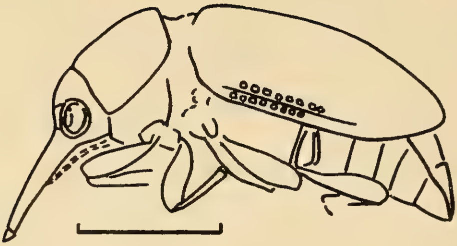

Fig. 90. *Oxycorynoides similis*, sp. nov.; holotype PIN No. 2554 / 713; Karatau, Upper Jurassic.

Epipleural margin of elytra almost straight. Rows of punctures on sides of elytra. Metathorax long, posteriorly more convex [in ventral view]. Abdomen with similar sternites, terminally pointed, projecting beyond elytral apex. Legs slender, short, tibiae apparently straight, tarsi not preserved.

Dimensions. Body length 3.0 mm, length of rostrum 0.8 mm.

Comparison. Distinguished by antennal attachment close to mid-rostrum.

Oxycorynoides brevipes L. Arnol'di, sp. nov.
(Figure 91)

Genus name coined from 'brevis' (Latin)—short, and 'pes' (Latin)—foot.

Holotype. No. 2239/1498*, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank

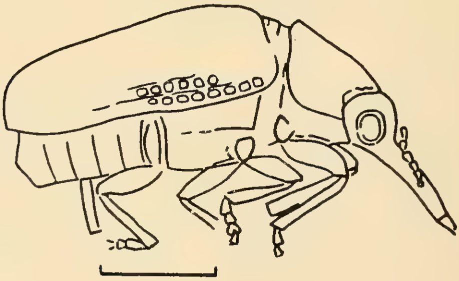

Fig. 91. *Oxycorynoides brevipes*, sp. nov.; holotype PIN No. 2239/1489; Karatau, Upper Jurassic.

*Given as 2239/1489 in Figure 91—General Editor.

of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head with noticeably convex frontal surface, forming an angle of approximately 100° with rostrum. Eyes rather large, positioned against base of rostrum, their width considerably more than basal thickness of rostrum. Rostrum scarcely shorter than pronotum, rather thick, slightly narrowing toward apex, weakly and uniformly curved, antennae attached slightly anterior to its middle, their first five segments small, remaining
161 segments not visible. Pronotum anteriorly projecting, dorsally very slightly convex, its base slightly raised medially. Elytra dorsally flat, rounded apically; epipleural margin almost straight, length two and a half times greater than that of pronotum. Rows of punctures visible on the sides of elytra (honeycomb pattern ?). Abdomen with similar sternites, last sternite bluntly rounded. Metathorax long, [ventrally] moderately convex posteriorly. Forelegs somewhat larger than remaining legs, femora slightly clavate, particularly middle and hind femora, tibiae straight and slender, tarsi small.

Dimensions. Body length 3.2 mm, length of rostrum 1.2 mm.

Comparison. Distinguished by slightly anteriorly projecting pronotum.

Oxycorynoides rohdendorfi L. Arnol'di, sp. nov.
(Figure 92)

Species named after B.B. Rohdendorf.

Holotype. No. 2239/1501, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

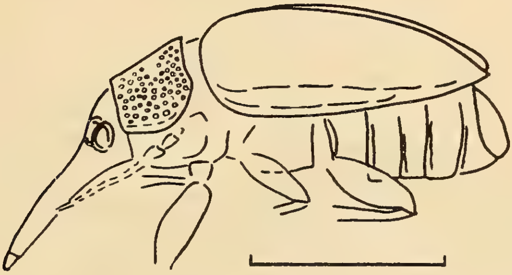

Fig. 92. *Oxycorynoides rohdendorfi*, sp. nov.; holotype PIN No. 2239/1501; Karatau, Upper Jurassic.

Description. Head small, with slightly convex frontal surface and rather small, noticeably anteriorly shifted eyes. Diameter of eyes less than basal width of rostrum. Rostrum rather thick, almost straight, its length 1.7 times that of pronotum, slightly thinning toward tip. Antennae attached a little anterior to midrostrum, slender; basal segments slightly varying in length; remaining segments poorly preserved, however a non-abrupt club distinguishable. Antennal apices reaching middle of pronotum. Pronotum small, anteriorly truncate, disk slightly depressed dorsally (result of fossilization ?), punctation dense and coarse. Elytra slightly convex dorsally, pointed apically, without noticeable sculpture. Metathorax long, [ventrally] slightly convex. Abdomen with similar sternites, fifth sternite covered by pygidium. Epipleural margin of elytra not curving above hind coxae, but uniformly rounded. Legs poorly preserved, but their structure undoubtedly normal, hind tibiae straight. Femora weakly clavate.

Dimensions. Body length 2.1 mm, length of rostrum 1.0 mm.

Comparison. Distinguished by anteriorly truncate pronotum.

Oxycorynoides ponomarenkoi L. Arnol'di, sp. nov.
(Figure 93)

Species named after A.G. Ponomarenko.

Holotype. No. 2066/2742, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

162 *Material.* Holotype.

Description. Head relatively large, round; eyes small, round, noticeably anteriorly shifted; rostrum straight, almost of uniform thickness, very slightly broadening only at tip, apparently cylindrical. Antennae attached slightly anterior to rostral middle, their total length scarcely more than that of rostrum,

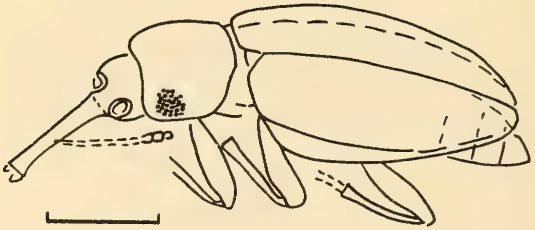

Fig. 93. *Oxycorynoides ponomarenkoi*, sp. nov.; holotype PIN No. 2066/2742; Karatau, Upper Jurassic.

club distinct, first segment not enlarged. Pronotum slightly emarginate*, posteriorly somewhat angularly projecting, disk with dense and fine punctation, laterally very weakly rounded. Elytra elongate-oval, posteriorly pointed, smoothly rounded laterally, without noticeable bend above hind coxae. [Ventral surface of] thorax not visible. Abdomen indistinctly visible, however having similar sternites, slightly projecting beyond elytral apex, and pointed at apex. Legs slender, femora long, slightly clavate; tibiae slender, straight; tarsi not visible.

Dimensions. Body length 3.9 mm, length of rostrum 1.0 mm.

Comparison. Distinguished by anteriorly emarginate and posteriorly projecting pronotum.

Oxycorynoides zherichini L. Arnol'di, sp. nov.

(Figure 94)

Species named after V.V. Zherikhin.

Holotype. No. 2239/1555, PIN, almost entire impression of beetle. South Kazakhstan. Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

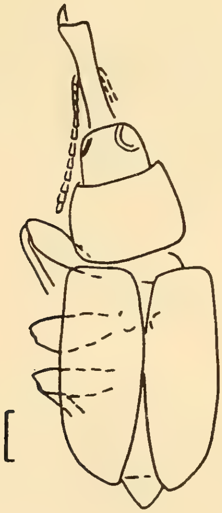

Fig. 94. *Oxycorynoides zherichini*, sp. nov.; holotype PIN No. 2239/1555; Karatau, Upper Jurassic.

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*Probably referring to the anterior margin. See *comparison* section —Scientific Editor.

Description. Head round, with small eyes placed closer to upper and anterior side of head capsule. Frontal surface apparently sharply descending to base of rostrum since head capsule is anteriorly bounded by arch, forming a small hood over the rostral base. Rostrum parallel-sided almost up to apex, moderately slender and angularly broadening only at apex itself. Its thickness equal to width of frons between the eyes. Antennae attached at midrostrum, slender, with scarcely enlarged first segment, and non-abrupt club, their length noticeably greater than rostrum. Pronotum transverse, slightly emarginate anteriorly and posteriorly, slightly rounded laterally. Elytra rather short and wide, apically right angled, laterally almost parallel-sided. [Ventral 63 surface of] thorax not visible, abdomen slightly projecting beyond apex of elytra, pointed. Legs with comparatively slightly thickened, short femora. As far as visible, tibiae slender and straight. Tarsi not visible.

Dimensions. Body length 3.0 mm, length of rostrum 1.0 mm.

Comparison. Distinguished by anteriorly and posteriorly emarginate pronotum, and short, wide elytra.

Remarks. Holotype lying on venter, hindering its comparison with other species.

Oxycorynoides progressivus L. Arnol'di, sp. nov.
(Figure 95)

Species name coined from 'progressio' (Latin)—progress.

Holotype. No. 2066/2317, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

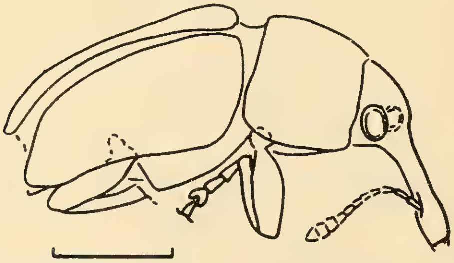

Fig. 95. *Oxycorynoides progressivus*, sp. nov.; holotype PIN No. 2066/2317; Karatau, Upper Jurassic.

Description. Head rather large; eyes round, placed closer to lower margin of head capsule. Rostrum not in same plane with lower surface of head capsule but forming a very obtuse angle with it. It is difficult to decide whether it is really so, or due to some twisting in the position of the head of this specimen that it [the rostrum ?][*] is visible both in dorsal and lateral views. Rostrum relatively short, slender in front of base, thinner than diameter of eyes, gradually broadening toward apex. Antennae attached in anterior third of rostrum, their basal segment scarcely larger than following segments; segments gradually increasing in thickness and transformation to club not abrupt. Pronotum with distinct anterior angles and weakly rounded sides, base almost straight. Elytra comparatively short, only 2.2 times longer than pronotum, their epipleural margin slightly excavated above hind coxae, posteriorly with blunt apical angle. Metathorax long, convex [ventrally]. Legs with rather short forefemora, slightly thickening; [fore-] tibiae also short, straight; [fore-] tarsi not shorter than tibiae, narrow. Hind femora not shorter than forefemora, slightly thickening; [hind] tibiae straight. Hind tarsi and middle legs not preserved. Unguiculate segment of foretarsi short and almost triangular.

Dimensions. Body length 3.4 mm, length of rostrum 0.8 mm.

Comparison. Distinguished by position of rostrum, distally shifted place of antennal attachment, and pronotum with distinct anterior angles.

Remarks. If the position of the rostrum is not the result of distortion during fossilization, then this species should be considered independent of other Jurassic rynchophoran beetles, and as transitional to forms having the rostrum situated medially on the head capsule. The marked apical shifting of the antennal attachment on the rostrum is also noteworthy. A slightly shifted position of the rostrum is noted in *O. similis* described above. *Oxycorynoides progressivus* probably belongs to an independent genus, standing somewhat closer to forms with rhynchitoid rostrums than implied by its specific name.

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Genus *Scelocamptus* L. Arnol'di, gen. nov.

Genus name coined from 'skelis' (Greek)—leg, and 'komptos' (Greek)—curved.

Type species. S. tenuirostris, sp. nov.; Upper Jurassic of South Kazakhstan.

Diagnosis. Small, convex bettles. In lateral view of specimen, rostrum typically belidoid, i.e., originating from lower part of head capsule, frontal surface forming an angle of 95–120° with upper surface of rostrum. Eyes small or large, rostrum smoothly curved, thinning toward apex, antennae

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[*] The discussion at the beginning of the *remarks* section, and the use of the feminine pronoun in the Russian original, imply that 'it' refers to the rostrum and not the entire specimen—Scientific Editor.

attached almost midrostrum, their first segment not elongate. Pronotum rather long. Elytra convex. Legs with moderately or markedly thickened femora and always with curved tibiae, particularly fore - and hind tibiae; tarsi small.

Species composition. Three species in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished by fore- and hind tibiae strongly curved in apical third.

Scelocamptus tenuirostris L. Arnol'di, sp. nov.

(Plate XIII, Photo 7; Figure 96)

Species name coined from 'tenuis' (Latin)—slender, and 'rostrum' (Latin)—beak.

Holotype. No. 2554/732, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site), Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head rather large, with slightly tuberculate frontal surface; eyes large, placed at sides of head capsule, closer to lower margin. Rostrum slender, rather long, but noticeably shorter than head capsule and pronotum together; tapering toward apex. Antennae attached midrostrum, their first two segments equal in length. Pronotum comparatively large, weakly emarginate anteriorly, middle of base with two angular projections evidently positioned against scutellum, which is not visible. Punctation noticeable on disk. Elytra more than three times as long as pronotum, with sharp apical angle. Lateral

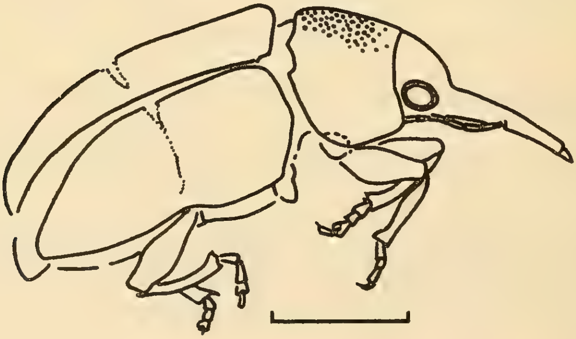

Fig. 96. *Scelocamptus tenuirostris*, sp. nov.; holotype PIN No. 2554 / 732; Karatau, Upper Jurassic.

margin strongly emarginate above hind coxae. [Ventral] Structure of thorax and abdomen indistinct; but, metathorax undoubtedly long and convex. Structure of abdomen unclear. Legs with moderately thickened femora, middle femora not thicker than hind ones; fore- and hind tibiae sharply curved in apical third (middle legs not preserved). Tarsi short, not thick.

Dimensions. Body length 3.6 mm, length of rostrum 1.1 mm.

Comparison. Distinguished by moderately thickened femora, fore-femora not thicker than hind ones.

165 *Scelocamptus curvipes* L. Arnol'di, sp. nov.
(Figure 97)

Species name coined from 'cuvus' (Latin)—curved, and 'pes' (Latin)—foot.

Holotype. No. 2384/512, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype. The beetle undoubtedly strongly distorted during fossilization and markedly flattened. Hence, all the less sclerotized parts are stretched out along the vertical axis, particularly in anterior half.

Description. Head large, high,* frontal surface forming an angle of approximately 100° with upper surface of rostrum. Eyes large, round, placed higher than upper side of rostral base. Rostrum short, thick, noticeably curved, gradually thinning toward apex. Antennae attached at end of basal third of rostrum. Their structure indistinct. Pronotum large, uniformly

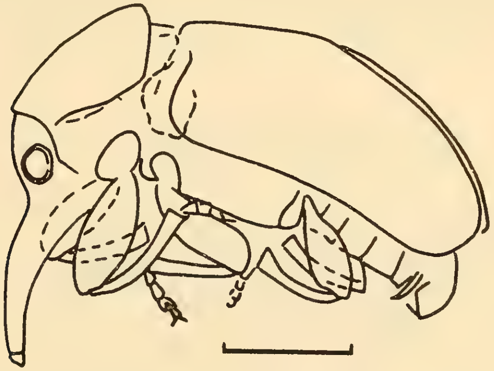

Fig. 97. *Scelocamptus curvipes*, sp. nov.; holotype PIN No. 2384/512; Karatau, Upper Jurassic.

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*See note at bottom of page 208—Scientific Editor.

moderately convex, anterior margin weakly emarginate. Elytra dorsally very gently convex, rounded apically, epipleural margin scarcely emarginate above hind coxae. Metathorax long, weakly convex [ventrally]; abdomen with similar sternites. Legs with strongly thickened forefemora, their width more than one-third the length. Middle and hind femora noticeably thinner, also hind femora shorter than forefemora. Fore- and hind tibiae rather strongly curved along their entire length, middle tibiae very slightly curved; tarsi small, slender.

Dimensions. Body length 4.0 mm, length of rostrum 1.3 mm.

Comparison. Distinguished by strongly thickened femora, hind femora shorter and thinner than forefemora.

Scelocamptus dubius L. Arnol'di, sp. nov.
(Figure 98)

Species name coined from 'dubius' (Latin)—doubtful.

Holotype. No. 2066/3037, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley. Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head small, diameter of eyes almost equal to basal width of rostrum; frontal surface of head capsule hardly visible from above, indistinct as it steeply descends to the upper surface of rostrum. Rostrum slightly thicker than distance between eyes, considerably shorter than head
166 capsule and pronotum together, slightly broadening apically. Owing to the semi-lateral position of the specimen, it is not clear whether the rostrum is curved, as in the preceding forms, or more or less straight. Antennae attached

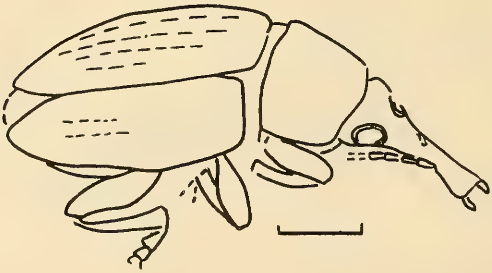

Fig. 98. *Scelocamptus dubius*, sp. nov.; holotype PIN No. 2066/3037; Karatau, Upper Jurassic.

almost midrostrum, length of first four segments equal. Pronotum slightly convex, with weakly projecting sides, widest in front of base, almost straight, anterior margin slightly angularly projecting. Elytra long, ovoid, with somewhat round presutural angle, disk with distinct punctate grooves. [Ventral surface of] thorax and abdomen not visible. Length of elytra 2.5 times that of pronotum. Legs with slender but not long femora. Fore- and hind tibiae noticeably curved along entire length; tarsi small.

Dimensions. Body length 4.6 mm, length of rostrum 1.8 mm.

Comparison. Distinguished by more slender femora.

Remarks. In general appearance this species most closely resembles members of the preceding genus, but its tibiae are distinctly curved, a fundamental feature of this genus.

Genus *Ampliceps* L. Arnol'di, gen. nov.

Genus name coined from 'amplus' (Latin)—large, and 'caput' (Latin)—head.

Type species. A. dentitibia, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Minute beetles, head highly convex frontally, forming less than a right angle with upper side of rostrum, its gular surface coplanar with lower side of rostrum. The latter rather thick and long, very slightly curved, thinning toward apex. Eyes small, placed higher than level of rostral attachment. Pronotum rather large, dorsally more or less flat. Elytra relatively short, with acute-angled presutural apices. Legs short, femora distinctly clavate; tibiae straight, short, with apical spurs.

Species composition. Two species in the Late Jurassic of South Kazakhstan.

Comparison. Distinguished by distinctly thickened femora and straight tibiae.

Ampliceps dentitibia L. Arnol'di, sp. nov.

(Plate XIV, Photo 1; Figure 99)

Species name coined from 'dens' (Latin)—tooth, and 'tibia' (Latin)—shin.

Holotype. No. 2239/1562, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Description. Head large, frontal surface forming somewhat less than right angle with rostrum, strongly convex. Eyes small, considerably less than
167 rostral width. Rostrum long, almost as long as head capsule and pronotum together, uniformly tapering toward apex, weakly and uniformly curved.

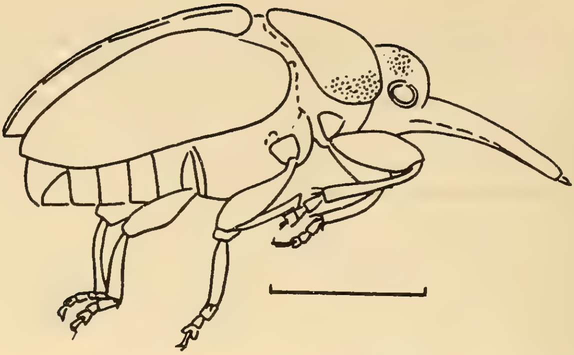

Fig. 99. *Ampliceps dentitibia*, sp. nov.; holotype PIN No. 2239/1562; Karatau, Upper Jurassic.

Place of attachment and shape of antennae not established. Pronotum with smooth anterior margin and rounded base, finely and densely punctate on disk. Elytra broad, with slightly curved epipleural margin and apices right-angled. Metathorax long, convex [ventrally]. Abdomen with similar sternites, pygidium present. Legs with short, moderately clavate femora, forefemora slightly longer than others, tibiae almost straight, a pair of spurs on inner angle of foretibiae, and apparently also on other tibiae but somewhat shorter. Tarsi slender, short, their first segment longer than remaining segments, unguiculate segment almost equal to it in length.

Dimensions. Body length 2.5 mm, length of rostrum 1.0 mm.

Comparison. Distinguished by longer head, and paired spurs on inner angle of foretibiae.

Ampliceps furcitibia L. Arnol'di, sp. nov.
(Figure 100)

Species name coined from 'furca' (Latin)—fork, and 'tibia' (Latin)—shin.

Holotype. No. 2239/1551, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head high*, but short; eyes small, less than basal width of rostrum; frontal surface of head capsule convex, forming an angle of about 80° with upper side of rostrum. Rostrum rather thick, slightly tapering toward apex, almost straight. Eyes placed above rostrum. Place of attachment and shape of antennae not clear. Anterior margin of pronotum slightly emar-

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*See our note on page 208—Scientific Editor.

ginate, base of pronotum very weakly excavated; disk with dense, moderately
large punctures. Elytra comparatively long, noticeably tapering toward apex,
2.2 times longer than pronotum, their apical angles acute. Epipleural margin
weakly excavated. [Ventral surface of] thorax and abdomen not visible. Legs
with short, moderately clavate femora; forefemora thickest; tibiae straight;
168 foretibiae longer than others, apically appearing bifurcate for a short distance
with spurs on outer and inner angles. Foretarsi slender, their first segment
larger than remaining segments. Middle and hind tarsi not preserved.

Dimensions. Body length 4.5 mm, length of rostrum 1.5 mm.

Comparison. Distinguished by high [= tall] but short head, and two spurs on opposite sides of tibial apex.

Genus *Paroxycorynoides* L. Arnol'di, gen. nov.

Genus name coined from genus *Oxycorynoides.*

Type species. P. elegans, sp. nov.; Upper Jurassic of South Kazakhstan.

Diagnosis. Body elongate. Head small, rostrum slightly tapering from base to midrostral antennal attachment, then broadening toward apex, apically slightly flared angularly. Mandibles small. Antennae with very slightly elongate first segment and non-abrupt three-segmented club, posteriorly almost extending to middle of pronotum. Pronotum transverse, with rather deep anterior emargination, sides uniformly rounded, base excavated. Elytra elongate, almost 3.5 times longer than pronotum, with acute apical angles.

Species composition. Monotypic genus.

Comparison. Differs from other representatives of the tribe in long and narrow body; unique rostrum; small, short pronotum, and long elytra.

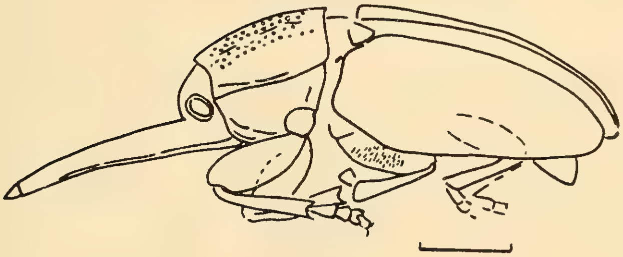

Fig. 100. *Amplicepsfurcitibia*, sp. nov.; holotype PIN No. 2239/1551; Karatau, Upper Jurassic.

Remarks. Owing to the position of specimen on its ventral side, a detailed comparison with other representatives of the tribe becomes difficult. Hence, its inclusion in this tribe is not verified.

Paroxycorynoides elegans L. Arnol'di, sp. nov.
(Plate XIV, Photo 2; Figure 101)

Species name coined from 'elegans' (Latin)—elegant.

Holotype. No. 2452/125, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Uspenskoe (Karatau-Galkino site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head small, round. Eyes small, less than basal width of rostrum shifted forward. Rostrum noticeably longer than head capsule and pronotum together. Pronotum round, tapering anteriorly, its posterior margin 1.8 times the anterior, maximum width of pronotum 1.7 times its medial length. Scutellum easily discernible, almost pentagonal. Elytra 1.7 times longer than maximum width. Abdomen projecting a little beyond apex of

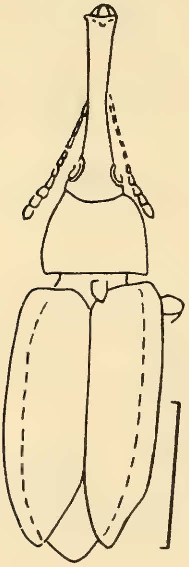

Fig. 101. *Paroxycorynoides elegans*, sp. nov.; holotype PIN No. 2452/125; Karatau, Upper Jurassic.

elytra. Legs, judging from the faint impression of part of middle femur, not thick.

Dimensions. Body length 3.1 mm, length of rostrum 1.1 mm.

169 Tribe ECCOPTARTHRINI L. Arnol'di, trib. nov.

Diagnosis. Small beetles. Rostrum rather long, antennae attached close to its middle. Pronotum transverse. Elytra broad. Legs short, femora thickened, first tarsal segment much larger than remaining segments, broad, almost bilobed, notched apically.

Composition. Tribe includes a single genus.

Comparison. Distinguished by completely abnormal form of foretarsi with very large, almost bilobed first segment.

Remarks. Enlargement of first tarsal segment also noted in some Jurassic belidoid Rhynchophora, but its structure in the latter is totally different.

Genus *Eccoptarthrus* L. Arnol'di, gen. nov.

Genus name coined from 'eccoptio' (Latin)—notched, and 'arthron' (Greek)—joint.

Type species. E. crassipes, sp. nov.; Upper Jurassic of South Kazakhstan.

Diagnosis. Head rather short. Antennae with small club. Pronotum very weakly transverse. Foretibiae curved.

Eccoptarthrus crassipes L. Arnol'di, sp. nov.
(Plate XIV, Photo 3; Figure 102)

Species name coined from 'crassus' (Latin)—thick, and 'pes' (Latin)—foot.

Holotype. No. 2239/1507, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Eyes shifted forward, frons between them almost the same width as base of rostrum. Rostrum preserved only in basal half, apparently rather long, place of antennal attachment close to midrostrum. Antennae only partially preserved, and had non-abrupt club. Punctation visible on head capsule. Maximum width of pronotum 1.2 times its length, its anterior margin rather deeply emarginate, posterior projecting backward at obtuse angle, laterally almost parallel, with rather coarse punctation. Elytra broad, with rows of punctures in grooves. Triangular scutellum visible between elytral bases. Legs with short, thick femora, forefemora thicker than remaining

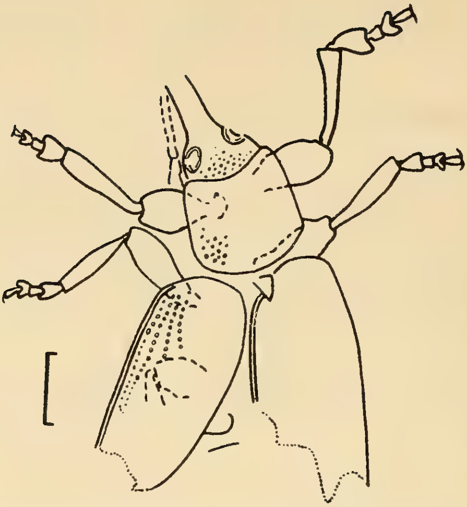

Fig. 102. *Eccoptarthrus crassipes*, sp. nov.; holotype PIN No. 2239/1507; Karatau, Upper Jurassic.

femora; foretibiae curved basally, straight further on middle tibiae slightly shorter, straight. First tarsal segment longer than the two following together.

Dimensions. Body length about 6 mm, rostrum longer than 1.5 mm.

170 Tribe DISTENORRHININI L. Arnol'di, trib. nov.

Diagnosis. Rostrum moderately long, noticeably constricted at place of antennal attachment, again constricted preapically or before base. Place of antennal attachment in anterior third or even anterior fourth of rostrum. Apex of latter slightly broadening, mandibles of usual size. Pronotum transverse. Elytra elongate, flat. Legs with poorly broadened femora.

Composition. Tribe includes single genus.

Comparison. Distinguished by unique structure of rostrum having two constrictions.

Genus *Distenorrhinus* L. Arnol'di, gen. nov.

Genus name coined from 'di' (Greek)—two, 'stenos' (Greek)—narrow, and 'rhinos' (Greek)—nose.

Type species. D. angulatus , sp. nov.; Upper Jurassic of South Kazakhstan.

Diagnosis. Head transverse. Rostrum almost as long as head and pronotum together. Pronotum transverse. Femora slightly thickened, tibiae straight, slender.

Species composition. Two species in the Late Jurassic of South Kazakhstan.

Remarks. A comparison of the two species in this genus shows significant differences in their rostral structure, and possibly their inclusion under one genus is provisional. *Distenorrhinus* has some features in common with the representative of the next subfamily, Brenthorrhininae, particularly the structure of the antennae and their nearly apical attachment.

Distenorrhinus angulatus L. Arnol'di, sp. nov.
(Plate XIV, Photo 4; Figure 103)

Species name coined from 'angulatus' (Latin)—angular.

Holotype. No. 2239/1547, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank

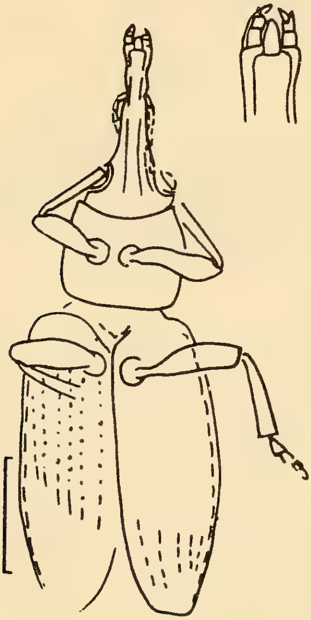

Fig. 103. *Distenorrhinus angulatus*, sp. nov.; holotype PIN No. 2239/1547; Karatau, Upper Jurassic.

of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Eyes strongly shifted forward. They were probably markedly convex. Rostrum almost as long as pronotum and head capsule together, tapering initially sharply, then gradually to the place of antennal attachment at the end of distal third of rostrum. Constriction rather sharp at antennal attachment, from which point for a short distance the rostrum again broadens, then again narrows. Second constriction somewhat weaker than first, apical expansion weak. Antennae poorly preserved, but their first segments obviously small. Pronotum weakly transverse, its anterior angles pointed and directed somewhat laterally; sides slightly rounded, anterior margin with shallow emargination, posterior margin straight, slightly narrower than
171 anterior. Elytra elongate, each three times longer than its maximum width, for two-thirds of length almost parallel-sided, with rounded apices, punctate grooves easily discernible, punctures small. Metathorax and abdomen not preserved. Legs slender, slightly thickening in the middle.

Dimensions. Body length 3.8 mm, length of rostrum 1.3 mm.

Comparison. Distinguished by the second rostral constriction more distal to the place of antennal attachment.

Distenorrhinus antennatus L. Arnol'di, sp. nov.

(Figure 104)

Species name coined from 'antenna' (Latin)—feeler.

Holotype. No. 2554/721, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Length of head capsule half its width at pronotal margin; eyes small, shifted forward; anterior margin of head capsule well differentiated, frontally steeply descending to rostral base. Rostrum noticeably longer than head capsule and pronotum together. Distance between anterior margins of eyes 1.6 times the thickness of rostrum. For a distance of one-fourth its length from base, rostrum briefly and shallowly constricted, then reattaining its former width, and further for about half its length gradually narrowing to the place of antennal attachment at the commencement of its distal fourth. Then rather noticeably broadening to apex. Apex of rostrum slightly broader than its base. Mandibles normal in size. Antennae long, their apices extending beyond middle of pronotum; first antennal segment one-and-a-half times longer than second; third twice the length of first; remaining segments elongate, scarcely shorter than first; club distinct, its last segment

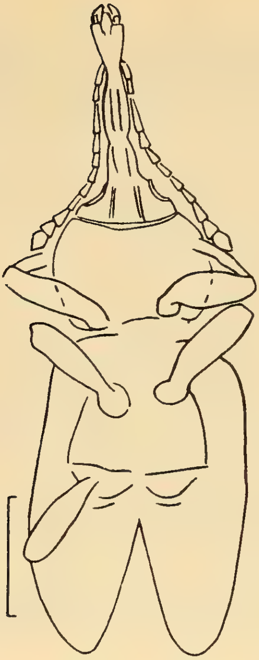

Fig. 104. *Distenorrhinus antennatus*, sp. nov.; holotype PIN No. 2554/721; Karatau, Upper Jurassic.

rhomboidal. Pronotum strongly transverse, its width 1.7 times its medial length, smoothly emarginate anteriorly and posteriorly, sides uniformly shallowly emarginate, undoubtedly flattened dorsoventrally. Elytra elongate, their length 3.3 times their maximum width, apically rounded. Metathorax long. Legs moderately long, femora weakly clavate.

Dimensions. Body length 4.0 mm, length of rostrum 1.3 mm.

Comparison. Distinguished by proximal position of second rostral constriction.

Subfamily Brenthorrhininae L. Arnol'di, Subfam. Nov.

Diagnosis. Rostrum short, thick, strongly broadening apically. Antennae attached at apex of rostrum. Mandibles large. Pronotum strongly transverse. Elytra parallel-sided, abdominal sternites similar.

172 *Composition.* Single genus.

Comparison. Distinguished by apical attachment of antennae.

Remarks. There is only one representative of this subfamily in the material studied by the author. Due to the impression being positioned on its dorsal surface, it is not possible to reliably establish the angle between the rostrum and head capsule (i.e., whether belidoid or not) nor whether distinct noto-pleural ridges were present on the pronotum. In general appearance the beetle somewhat resembles brentids. The structure of its rostral apex very closely resembles that observed in males of Recent brentids. The antennal structure has no correspondence in Recent species of the family, and is absolutely unique.

Genus *Brenthorrhinus* L. Arnol'di, gen. nov.

Genus name coined from genus *Brenthis*, and 'rhinos' (Greek)—nose.

Type species. B. mirabilis, sp. nov. Upper Jurassic of South Kazakhstan.

Diagnosis. Head large, transverse; rostrum noticeably shorter than head capsule and pronotum together, thick, sharply broadening apically, its thickness equal to one-fourth its length. Antennae attached at very corners of rostrum, their first segment strongly arched and only slightly shorter than apical width of rostrum, second one-third, the length third straight and as long as first, remaining segments twice as long as wide, club non-abrupt but distinct. Pronotum dilated, anteriorly rather strongly emarginate, with distinct ridge, i.e., having narrow constriction. Elytra parallel-sided, with right-angled apices. Metathorax long, three times the length of hind coxae. Abdomen with similar sternites. Legs long, femora rather strongly thickened, forefemora larger than others; tibiae thin, very slightly curved in anterior half, with short apical bristles.

Species composition. Monotypic genus.

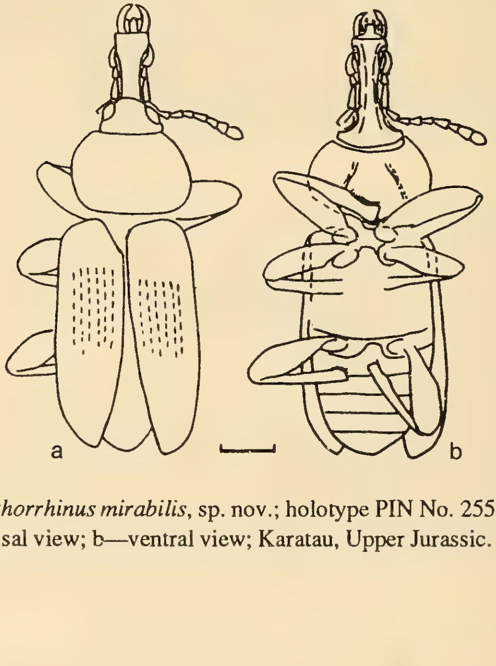

Fig. 105. *Brenthorrhinus mirabilis*, sp. nov.; holotype PIN No. 2554/708: a—dorsal view; b—ventral view; Karatau, Upper Jurassic.

Brenthorrhinus mirabilis L. Arnol'di, sp. nov.
(Plate XIV, Photo 5; Figure 105)

Species name coined from 'mirabilis' (Latin)—remarkable.

Holotype. No. 2554/708, PIN, almost entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley, Aulie area near Mikhailovka village (Karatau-Mikhailovka site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Mandibles only slightly shorter than apical width of rostrum. Mentum visible between them, anteriorly extending up to almost half the length of mandibles. Head capsule laterally transforming stepwise 173 into rostrum. Third antennal segment reaching [back to] this step, whence the antennae, instead of running parallel to rostrum, turn at an angle as in geniculate antennae of Recent forms, though in this specimen they are certainly not geniculate. Prosternum with broad process between forecoxae, posterior angles completely rounded. Abdomen slightly shorter than large metathorax. Elytra with slender punctate grooves.

Dimensions. Body length 6.7 mm, width at shoulders 2.6 mm, length of rostrum 1.7 mm.

Subfamily Nanophydinae L. Arnol'di, Subfam. Nov.

Diagnosis. Rostrum slightly curved, with antennae attached at middle. Metathorax very short. Fourth abdominal sternite with posterior angular notch.

Composition. Single genus.

Comparison. Distinguished by characteristic structure of abdomen with angularly notched fourth sternite, and short metathorax.

Genus *Nanophydes* L. Arnol'di, gen. nov.

Genus name coined from genus *Nanophyes*.

Type species. *N. ovatus*, sp. nov. Upper Jurassic of South Kazakhstan.

Type species. Body small, short and wide, its general configuration oval. Head large. Rostrum rather long, curved. Pronotum short. Metathorax approximately one-third of abdomen in length. First three abdominal sternites of normal structure, fourth short, posteriorly with wide deep emargination into which obtuse angle of fifth sternite fits.

Species composition. Monotypic genus.

Remarks. The shortened metathorax and shape of body strongly suggest that this form had lost the ability to fly.

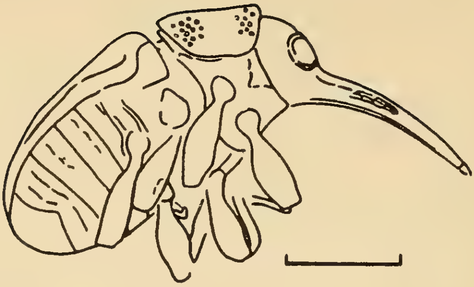

Fig. 106. *Nanophydes ovatus*, sp. nov.; holotype PIN No. 1789/102; Karatau, Upper Jurassic.

Nanophydes ovatus L. Arnol'di, sp. nov.
(Plate XIV, Photo 6; Figure 106)

Species name coined from 'ovum' (Latin)—egg.

Holotype. No. 1789/102, PIN, entire impression of beetle. South Kazakhstan, Chimkent oblast, Algabass region, south-western flank of Kashkarata river valley. Uspenskoe village (Karatau-Calkino site). Upper Jurassic, Karabastau series.

Material. Holotype.

Description. Head large; eyes small, placed above upper side of rostrum. Length of rostrum noticeably exceeding length of head capsule and pronotum together; rostrum strongly but gradually tapering toward apex, and gently curved all along entire length; antennal attachment close to midde. Pronotum short, with large sparse punctures, posterior angles rounded. Judging from 174 the shape of metathorax and abdomen, the elytra were short and wide, with distinct epipleura. Legs comparatively short, with slightly clavate femora, and apparently straight, slender tibiae.

Dimensions. Body length 3.0 mm, length of rostrum 1.6 mm.

* * *

The author acknowledges the fact that the classification of Eobelidae followed above is largely tentative and partly artificial. The main reason for this is the nature of the material itself. The fossil beetles studied in this work represent a more or less random selection from the entire fauna. Moreover, this material did not fossilize simultaneously but over some period of time that was extremely long from the viewpoint of an entomologist studying extant fauna. Another point of great significance is that generally it is not possible to study the entire repertoire of taxonomic characters, but only those which are visible in an impression.

However, the persistence of the main structural features of all the Jurassic Rhynchophora studied, excluding a few doubtful cases not differing from those of the above described primitive type, cannot be incidental. This certainly reflects a definite evolutionary level which this already highly specialized group of Coleoptera had achieved.

The overall primitiveness of Eobelid morphology has already been established; this family combines within it the most primitive characters which are individually preserved in various extant groups of Rhynchophora presently having the status of independent families. The individual characters [taken in combination] are peculiar to the fossil forms. [The preceding observations] definitely support the idea of a common origin for what is currently an enormous group. Based on general appearance and most of the main characters, the Late Jurassic Rhynchophora most closely resemble the primitive representatives of the Recent family Belidae. Therefore, they may tentatively be considered the "beloidoid"* phase of rhynchophoran evolution.

Among the Late Jurassic Rhynchophora, the most stable morphological structure is the rostrum. This structure, the main diagnostic feature of the group, arose much earlier and reached a high level of specialization in the Late Jurassic. The author suggests that the development of the rostrum assisted the group in becoming the largest of all in the order Coleoptera, since it made it possible for the preimaginal stages to develop within the plant tissues or under their cover. This provided the larvae with an abundance of high-quality food, more or less constant optimal atmospheric humidity and probably a significant reduction in the pressure of predators and parasites. In the Late Jurassic forms studied, the rostra are of the same type with a solitary exception, and are closest in structure to those of Recent Nemonychidae or Rhynchitinae of the family Attelabidae. The rostrum of *Brenthorrhinus* differs most significantly from this type: it is short and thick, with an apical attachment of the antennae, a feature now more characteristic of species with terrestrial larvae. However, its structure is very similar to that in males of some Brentidae, and is probably a secondary sexual character as is true for the highly enlarged mandibles. In detail, the rostrum of the studied Late Jurassic forms has a rather varied structure and probably reflects the frequent species or group adaptations to different plant species or different plant parts. It must be emphasized again that the studied examples of Late Jurassic Rhynchophora have a lower placement of the rostrum, which is presently characteristic only of the relictual family Belidae. All the remaining Recent families have a middle or upper position of the rostrum. The middle position is characteristic of the most morphologically primitive families: Nemonychidae, Oxycorynidae, Attelabidae (subfamily Rhynchidae), and a few others. All of the extant Curculionidae have an upper position of the rostrum.

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*So given in the Russian original. In the context of its reference to the family Belidae it would be more correct to say "belidoid"—General Editor.

Among the Recent forms, the notopleural ridge has only been preserved 175 in a few Oxycorynidae (also a relict family). In a few Curculionidae a faint blunt ridge is present laterally on the pronotum, but there is never a sharp flange and notopleural suture. It is interesting to note that the notopleural ridge and suture are absent in the extant Belidae.

The antennae of Eobelidae are closest to those of the Recent Attelabidae (subfamily Rhynchitinae) or to Nemonychidae. They always have a loose and indistinct three-segmented club which is absent in the extant Belidae.

The aforementioned facts strongly suggest that the Mesozoic Rhynchophora of the "Belidoid" type (having a low position of the rostrum) later became extinct to a large extent, leaving behind a dead-end, relictual group: the extant Belidae. It is hardly possible to trace direct descendants of the already specialized Jurassic Rhynchophora among the Recent curculionids.The Late Jurassic rhynchophoran fauna, apparently rich in species, fed on different plants of their period and had diverse trophic relationships which are reflected in the varied types of rostra, legs, and general body shapes. However, judging from the present-day associations of curculionids, it may be assumed that their trophic relationships with Cryptogams were never widespread, and the rare modern occurrences represent a secondary adaptation.

Several general conclusions pertaining to the further evolution of the Rhynchophora can be drawn from the study of the available material. Based on the general structure of the elytra and their deformation during fossilization, it may be assumed that the elytra of the Jurassic Rhynchophora were relatively weakly sclerotized and mostly flattened. More durable structures were the prothorax, mesothorax, metathorax, and head, particularly the rostrum. The subsequent independent evolution of all representatives of the group proceeded in parallel toward a greater degree of sclerotization, greater convexity of the elytra and prothorax, and disappearance of the notopleural ridge. The abdomen of most of the Rhynchophora lost the homonomic structure of the sternites, all of which, except the first, were evidently movable. In the vast majority of extant Rhynchophora, the first two sternites are partially or completely fused and occupy more than half the length of the abdomen; mobility has been retained only in the abdominal apex. The fusion of many sutures in the thoracic region proceeded in parallel. It may be speculated that all these modifications occurred under the influence of general climatic aridity, as well as the increasing pressure of entomophages.

The position of the antennal attachment was markedly different in most of the Jurassic species examined. It was near the midrostrum, rarely close to its apex, but never at its base. In the extant belids and oxycorynids, on the contrary, the antennae are always attached to the base of the rostrum or in its proximal third (Belidae). The disappearance of the antennal club is noteworthy in the Recent Belidae, the Jurassic ancestors of which always had a distinct (though not abrupt), loose club of the "rhynchitoid" type. Based on the absolute predominance of a well developed club among the extant Rhynchophora, this structure can be considered advanced; the reasons for its reduction in the Recent Belidae are unclear.

As previously mentioned, the belidoid type is distinctly predominant among the studied examples of Jurassic Rhynchophora. However, several forms, while preserving the fundamental archaic belidoid characters, are markedly similar to the most primitive of the extant oxycorynids, particularly in the structure of the pronotum and the general body shape. More rarely, they are similar to the Recent Nemonychidae and Rhynchitinae of the family Attelabidae. None of the aforementioned groups, which deviated from the generalized belidoid type, can be considered as a main evolutionary line equal in importance to the latter. Judging from the available material, these forms which deviated from the belidoid group never flourished, and therefore cannot be rated as its "sister" group. Thus, within the [deviant] group, several evolutionary branches arose simultaneously. These may be regarded as a "cluster" of new lines of specialization, and not [the result of] a dichotomous
176 branching [which would have yielded] a new sister group (sensu Hennig, 1969) of equivalent status [to the generalized belidoid line].

It should be emphasized again that all the descendant groups of the Rhynchophora complex that flourished in the Late Jurassic are now represented only by small relictual families. There is as yet not adequate data for establishing the time of separation from the "belidoid" stock of the forms which could be considered representatives of the extant Curculionidae.

In his interesting review of paleogeographic data on insects, Zherikhin (1970) prefers to group the Late Jurassic Rhynchophora with the family Oxycorynidae and only to a lesser degree with Belidae. However, many of the abovenoted structural features of the Jurassic species, which are most important to explain the taxonomic affinity of these insects, force us to consider them as representatives of a separate family, now extinct, which is closest to the Recent Belidae but has several characters of the family Oxycorynidae as well as Nemonychidae and Attelabidae.

Plesiomorphic characters have never been observed simultaneously in a more or less complete "selection" of the Recent relict Rhynchophora. However, a set of the more important ones (for example, the structure of the head capsule and rostrum, or the structure of pronotum, etc.) characterizes each of the extant families. On the other hand, within a complete range of the Late Jurassic Rhynchophora all the plesiomorphic characters are usually simultaneously present, a reaffirmation of the monophyletic origin of the Rhynchophora.

Family ATTELABIDAE Billberg, 1820

Subfamily Rhynchitinae Thomson, 1859

Tribe AULETINI Reitter, 1912

Genus *Baissorhynchus* Zherichin, gen. nov.

Genus name coined from Baisa river, and 'rhynchos' (Greek)—rostrum.

Type species. B. tarsalis, sp. nov. Lower Cretaceous of Trans-Baikal.

Description. Head short, hemispherical, transverse, lacking constriction beyond eyes. Temples short. Eyes large, round, lateral. Gular suture apparently medial. Rostrum long, rather slender, cylindrical, uniformly and rather strongly curved, with transverse depression at junction with head. Labrum labular, free. Prosternum without traces of sutures. Elytra slightly convex, with steep, almost vertical slope, covering pygidium, with irregular rows of punctures. Epipleura reduced, but distinct. External basal angle of elytra oblique. Wings normally developed. Forecoxae conical, approaching posterior margin of prosternum. Middle coxae spherical, contiguous. Femora short, rather broad, lacking armature. Tibiae same length as femora. Tarsi with bilobed, deeply cleft second and third segments; true fourth segment not visible.

Species composition. One species in Early Cretaceous of Trans-Baikal.

Comparison. Differs from all the known genera of the tribe in the deeply cleft, bilobed second tarsal segment, similar in shape to third. [Also differ in possessing] a free labrum, short temples, and irregular rows of punctures on elytra instead of usual scattered punctation. Scattered punctation is present on earlier described genera with the exception of *Car* Blackb. from which *Baissorhynchus* is distinguished by strongly curved rostrum, and considerably shorter and thicker legs as well as a [different] structure of tarsi.

Remarks. The state of preservation of the holotype *Baissorhynchus tarsalis* Zherichin sp. nov., does not permit the clarification of certain taxonomically important structural details. Among the characters available
177 for study, the structure of labrum is very important. A free labrum is present only in a few Curculionoidea, viz., Rhinomaceridae, Anthribidae, Platypodidae, some Attelabidae (taking the latter family in the sense suggested by R. Crowson, 1955), and also in an anomalous genus *Anchylorrhynchus* Fahr. from the family Curculionidae (Voss, 1943). A long rostrum is never observed in the families Anthribidae and Platypodidae. The presence of distinct elytral epipleura argues against the inclusion of *Baissorhynchus* in Curculionidae. It must therefore be included in either Rhinomaceridae or Attelabidae which it even resembles in general appearance. The main distinguishing characters by which one can reliably separate representatives of these two families (structure of mandibles and maxillary palps) cannot be established from the available remains or the wing venation. The nature of

the gular suture supports the inclusion of *Baissorhynchus* in Attelabidae. This suture is paired in all the known Rhinomaceridae, whereas in Attelabidae only one medial suture is present. There is no trace of the paired gular suture on the medial cleavage line on the head of the *Baissorhynchus tarsalis* holotype; it is assumed that it was medial and proceeded along the cleavage line.

Judging from the shape of the head and rostrum, *Baissorhynchus* must be included in the subfamily Rhynchitinae of the family Attelabidae. Comparative characters draw it close to the isolated genus *Car* Blackb. (four contemporary species from Australia, and one from the Paleogene of Europe). *Car* also exhibits several other characters distinguishing it from the remaining Rhynchitinae—such as simple free claws, basally attached antennae and free abdominal sternites—but unfortunately it is not known whether *Baissorhynchus* also possessed them. Since the genus *Car* is not known to us in nature and its comprehensive comparison with *Baissorhynchus* is out of question, it seems reasonable to postpone separating these general into a special taxon and retain them in the tribe Auletini of the subfamily Rhynchitinae, where *Car* was placed by Crowson (1955). It is noteworthy that the structure of the tarsi in *Baissorhynchus* is different from that in Attelabidae and Rhinomaceridae, but resembles that in oxycorynids.

Baissorhynchus tarsalis Zherichin, sp. nov.
(Plate XIV, Photo 7; Figure 107)

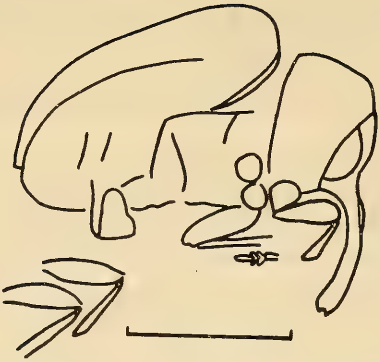
Species name coined from 'tarsus' (Latin)—foot.

Holotype. No. 1989/3010, PIN, reverse impression of almost entire beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river, downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Zazin series.

Material. Holotype.

Description. Rostrum equal in length to head and pronotum together, with very fine dorsal rugae basally. Punctation on head fine, rather dense. Pronotum not longer than its basal width, apparently faintly bi-emarginate, dorsally almost flat, steeply sloping anteriorly just before anterior margin. Punctation of pronotum large and dense; on sides almost partially fused into
178 transverse rugae. Punctures on elytra large, dense. Distance between punctate rows not exceeding diameter of punctures. Tibiae straight. Tarsi slightly shorter than tibiae, their first segment broad, second and third equal to it in length, unguiculate segment almost equal in length to remaining segments together. Sides of thorax and at least base of abdomen with dense coarse punctures.

Dimensions. Body length (without rostrum) 2.2 mm.



177 Fig. 107. *Baissorhynchus tarsalis*, sp. nov.; holotype PIN No. 1989/3010; Baisa, Lower Cretaceous.

Family CURCULIONIDAE Latreille, 1802

Subfamily Nanophyinae Seidlitz, 1891

Genus *Cretonanophyes* Zherichin, gen. nov.

Genus name coined from 'creta' (Latin)—chalk, and genus *Nanophyes*.

Type species. *Cretonanophyes longirostris*, sp. nov. Lower Cretaceous of Trans-Baikal.

Description. Rostrum very long, delineated from head by a depression*. Eyes large, round. Frons rather wide, without tubercle. Antennae geniculate with thick six (or possibly seven) segmented flagellum. Pronotum apparently with narrow basal slope. Scutellum clearly visible. Elytra with well developed humeral tubercles, without tubercles on disk or lateral flanges. Forecoxae reaching anterior margin of prosternum. Trochanters large. Femora without denticles. Tibiae longer than femora, slender, straight, not apically broadening. Second tarsal segment slightly bilobed. Claws slender, free, without denticles, equal in length. Third and fourth abdominal sternites strongly truncate. Pygidium free.

Species composition. One species in Early Cretaceous of Trans-Baikal.

Comparison. Differs from all the known genera of the subfamily in broader frons; thickened flagellar segments of antennae, equal in width to apex of scape; clearly identifiable scutellum, and bilobed second tarsal segment. Among the present-day Nanophyinae, free claws are present only in the genus *Corimalia* Gozis. However, the species of this genus usually possess a four- or five-segemented antennal flagellum; if six-segmented then

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*The term 'depression' as given here does not refer to a pit or groove, but rather to a drop-off or down-step—Scientific Editor.

the femora are always with denticles. Antennal flagella in *Ctenomerus* Schoenh., *Hexatmetus* Marshl. and *Diplophyes* Marshl. also consist of six segments, but in all representatives of these genera the claws are fused and the femora have denticles. *Cretonanophyes* differs further from *Hexatmetus* Marshl. in the developed humeral tubercles of the elytra. The genus *Nanomicrophyes* Pic, having free claws, is related not to Nanophyinae but to Tychiinae. In appearance, *Cretonanophyes* is most similar to species of the extant genus *Ctenomerus* Schoenh. (tropical Africa and Asia).

Remarks. The combination of geniculate antennae together with enlarged trochanters undoubtedly indicates the affiliation of *Cretonanophyes* to the subfamily Nanophyinae, family Curculionidae. This is also confirmed by the characteristic inequality of the abdominal segments.

Cretonanophyes longirostris Zherichin sp. nov.
(Plate XIV, Photo 8; Figure 108)

Holotype. No. 1668/1772, PIN, almost entire impression of beetle: Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river, downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Zazin series.

Material. Holotype.

Description. Head rounded, with fine, sparse punctures. Rostrum almost twice (7 : 4) as long as head together with pronotum, slender, cylindrical, 179 weakly and uniformly curved, with sparse punctation basally, in apical part smooth or possibly with microscopic punctures. Antennae attached somewhat behind midrostrum. Scape short, not reaching base of rostrum, slender, thickening club-like toward apex, curved. First two flagellar segments identical, longer than wide; third segment shorter than the two preceding; fourth longer than third; fifth and sixth identical, slightly broader than preceding ones, equal in length and width. Pronotum apparently not longer than wide, convex, greatest height posterior to middle, dorsally and laterally with sparse, fine punctures. Elytra rather strongly and uniformly convex, with rows of sparse, large punctures. Intervals between them wider than diameter of punctures, apparently with weak transverse rugae. Legs with dense, slender, rather long, oppressed pubescence. Tarsi shorter and wider than tibiae, their second segment longer than wide, third shorter than second, unguiculate segment shorter than second and third together.

Dimensions. Body length (without rostrum) 3.1 mm.

Subfamily Slonikinae Zherichin, Subfam. Nov.

Diagnosis. Rostrum long, slender, cuneately narrowing toward apex, apically pointed. Antennal sockets directed toward eyes. Antennae not geniculate, with loose club, consisting of individual rounded segments, attached in distal

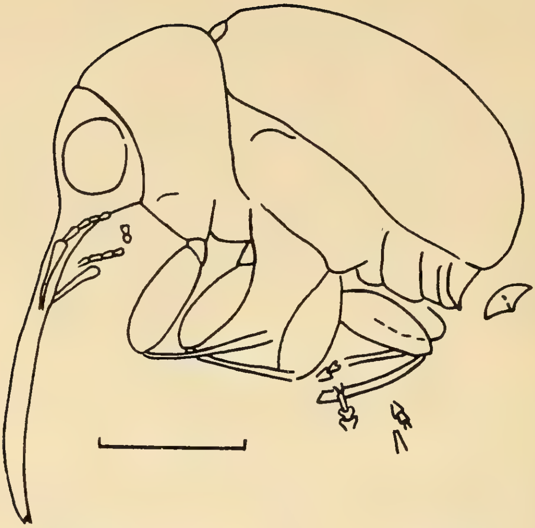

Fig. 108. *Cretonanophyes longirostris*, sp. nov.; holotype PIN No.1668/1772; Baisa, Lower Cretaceous.

half of rostrum. Prothorax with distinct lateral slope, without a groove for insertion of rostrum. Elytra with punctate grooves. Forecoxae attached at posterior margin of prosternum, contiguous. Middle coxae convergent. Metathorax equal in length to first abdominal sternite; Trochanters small. All femora identical, not thickened. Tibiae with projecting outer apical angle. Abdominal sternites slightly varying in length.

Composition. One genus in Early Cretaceous of Trans-Baikal.

Comparison. Differs from most subfamilies of Curculionidae in nongeniculate antennae; from Apioninae (having similar antennae) in short trochanters and loose club; from Brachycerinae in long rostrum; from Rhynchaeninae in not thickened hind femora, rostrum not curved under body, and apical process on tibiae; from Cryptoderminae in antennal attachment far from rostral base, loose club, and elongate linnear antennal grooves. 180

Remarks. Genus *Slonik* undoubtedly belongs to the family Curculionidae and has several archaic distinguishing characters (nongeniculate antennae, loose club not clearly demarcated from flagellum, and lateral slope of prothorax). In appearance it resembles some Tychiinae (for example, genus *Tychius* Cerm.), but the latter has no species with nongeniculate antennae; moreover, the drawn out posterior corners of the middle abdominal sternites are characteristic of them. Among the families with first antennal segment short, *Slonik* slightly resembles only Cryptoderminae. This is a relict group including one oriental and one African genus. However, Cryptoderminae is an advanced group, aside from [possessing] the aforementioned plesiomorphs, and is a derivative of Rhynchophorinae; the reduction of the first antennal segment is clearly secondary in Cryptoderminae.

Genus *Slonik* Zherichin, gen. nov.

Name of the genus is a Latinized Russian word.*

Type species. S. sibiricus, sp. nov. Lower Cretaceous of Trans-Baikal.

Description. Head spherical, ventrally strongly convex. Temples very short. Frons wide, wider than diameter of eyes. Rostral junction with frons without depression**. Antennae slender, rather long, reaching posterior margin of eyes. Scutellum large, triangular. Elytra keel-shaped, tapering posteriorly with distinct rows of punctures. Humeral tubercles well developed. Lateral margins of elytra straight. Prothorax anteriorly with small hood, separated by shallow groove. Posterior margin of abdominal sternites straight. Fifth sternite longer than others. Pygidium completely covered by elytra. Femora without armature, without apical constriction. Tibiae slender, straight, gradually broadening toward apex.

Composition. One species in Early Cretaceous of Trans-Baikal.

Slonik sibiricus Zherichin, sp. nov.
(Plate XIV, Photo 9; Figure 109)

Species named after Siberia.

Holotype. No. 1989/2938, PIN, direct reverse impressions of entire body of well-preserved beetle. Trans-Baikal, Buryat ASSR, Eravnin region, left bank of Vitim river, downstream from the mouth of Baisa river (Baisa site). Lower Cretaceous, Zazin series.

Material. Holotype.

Description. Head with dense, coarse punctures. Eyes elongate; rostrum equal in length to head and pronotum together, strongly and uniformly curved, with slender keel above antennal sockets. Punctation of rostrum rather dense and coarse. Antennae attached at one-third length of rostrum 181 from its apex. Their first six segments almost identical, cylindrical, considerably longer than wide. Seventh and eighth segments slightly broader and considerably shorter, almost not longer than wide. Ninth rounded, broader than eighth, but narrower and shorter than the following two. These last are markedly enlarged, rounded. Pronotum flat, with straight posterior margin, and dense, coarse punctation. Elytra flat, sloping from base to apex, with rows of sparse large punctures. Intervals between them broader than diameter

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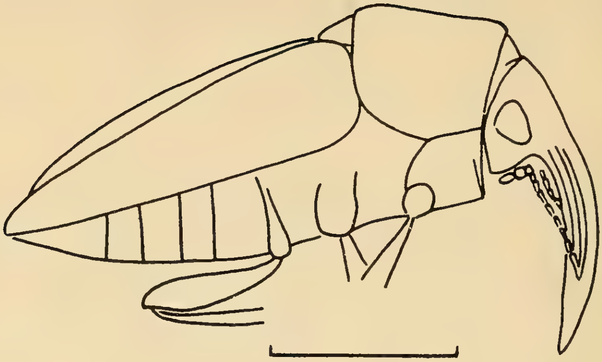
*'Slonik' is a transliteration of the Russian word which means 'little elephant'. This term is often applied to weevils—Scientific Editor.

**See comment on bottom of p. 244—Scientific Editor.



180 Fig. 109. *Slonik sibiricus*, sp. nov.; holotype PIN No. 1989/2938; Baisa, Lower Cretaceous.

of punctures. Prothorax with transverse rugose punctures. Punctation of meso- and metathorax and abdomen dense and rather coarse. Body dark colored, antennae and legs light colored, antennal clubs dark.

Dimensions. Body length (without rostrum) 3.1 mm.

REMARKS ON THE PHYLETIC LINKS AND ECOLOGY OF BAISIAN RHYNCHOPHORA

Three families of Rhynchophora are represented in the Early Cretaceous Baisian fauna: Eobelidae (two undescribed species), Attelabidae (one species) and Curculionidae (two species). The first of these is characteristic of the Mesozoic and is known from the Triassic and Jurassic; the other two first appeared in the Neocomian. They [Attelabidae and Curculionidae] are represented by special archaic genera; the two species of Curculionidae belong to two widely separated branches of the family. Both these branches occupy a rather special taxonomic position and have already been differentiated by various authors into independent families on the basis of comparative morphological and anatomical studies of the extant forms (Apionidae and Rhynchophoridae). While the independence of the family Apionidae is supported by many authors, the separation of the Rhynchophoridae—established by Morimoto (1962)—has not yet been widely accepted. In Baisa, the first group ["Apionidae"] is represented by the genus *Cretonanophyes*. The second apparently includes the genus *Slonik*, although a strict justification for its inclusion in the "Rhynchophoridae" is not possible on the basis of the available material since many important distinguishing characters (structure of mouth parts, abdominal terga, genitalia) are not available for study in the holotype of *Slonik sibiricus*. If *Slonik* is in fact included in this group, then the main line of "Rhynchophoridae" could have separated from Eobelidae independent of the other Curculionidae as early as the Late Jurassic or Early Cretaceous, in which case it definitely merits isolation into a separate family. On the other hand, “Apionidae” is differentiated from other higher Curculinoidea by several plesiomorphic characters and by only a few secondary apomorphic ones such as elongation of the trochanters. Hence it is difficult to be certain of the independence of apionids. Instead they may simply be regarded as one of the least evolutionarily advanced groups of Curculionidae, and probably even the ancestors of this family. The discovery that *Cretonanophyes* has a rather complete set of plesiomorphic characters for Curculionidae confirms this interpretation of “Apionidae”. Since the present material does not provide a basis for dividing Curculionidae into several families, it seems advisable to tentatively adopt a broad range for this group, encompassing the “Rhynchophoridae” and “Apionidae”. Therefore, *Cretonanophyes* and *Slonik* are included in Curculionidae. It is hoped that an investigation of material from other Mesozoic sites will resolve this tangle.

Very little can be said about the ecology of the described species. The mode of life of *Car* is unknown although Voss (1953) suggests that it was associated with conifers; possibly *Baissorhynchus* developed on conifers as well. It is impossible to judge the trophic relations of *Slonik*. There are grounds for suggesting (in analogy with many extant representatives of rhynchophoroid stem groups, and based on their general appearance that it was associated with wood; probably either dead or decomposing wood. However, in the first place, the inclusion of *Slonik* in this main line is not fully substantiated; and secondly, even if it belongs, there are such marked differences from the extant representatives that an analogy with them might 182 prove incorrect. With regard to *Cretonanophyes*, its larvae probably lived on the generative organs of some angiosperms. Among the present-day Nanophyinae there is one genus (*Nanodiscus* Kiesw.) associated with *Juniperus* and *Thuja*, but this relationship is probably secondary. Gall-forming Nanophyinae are known, but they largely belong to the advanced groups of the subfamily, suggesting that their infestation of fruit is primary. The spectrum of food plants of representatives of the subfamily is extremely wide (Ericaceae, Tamaricaceae, Dipterocarpaceae, Lythraceae, Crassulaceae, Ebenaceae, and others). Therefore, it is impossible to be precise about the taxonomic position of the host plant of *Cretananophyes*. Representatives of one group of insects associated with Angiospermae, viz. Cephidae (Hymenoptera), have already been described from Baisa (Rasnitsyn, 1969). Rasnitsyn suggested the existence of angiosperm flora in Baisa at a time when their remains were still unknown from this site. In 1969, during an expedition of the Paleontological Institute, Academy of Sciences, USSR, to Baisa, remains of dicotyledons of uncertain taxonomic position were collected (Vakhrameev, 1973). This discovery was proof of the existence of flowering plants in the Neocomian of Trans-Baikal, and confirmed the validity of predictions based on studies of the entomofauna. Insects associated with angiosperms, and insect-host plant associations in general, are few in Baisa. The host plants probably occurred there in limited quantities. The activity of insects favors their burial over that of their host plants, and from the composition [of the insect fossils] one can quite frequently judge the flora of territories somewhat removed from the water bodies in which the insects were buried. In several instances, the composition of the entomofauna may be the sole source of this type of information.

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PLATES

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PLATE I

Families Triaplidae, Parahygrobiidae and Coptoclavidae

1 and 2. *Triaplus macroplatus*, sp. nov. (c).
  1—Holotype PIN No. 2971/104 (× 7.5); 2—Paratype PIN No. 2905/24 (× 8); Madygen, Triassic.
3. *Triaplus laticoxa*, sp. nov. (c).
  Paratype PIN No. 2555/1720 (× 4.5); Dzhailyaucho, Triassic.
4. *Parahygrobia natans* sp. nov. (c).
  Holotype PIN No. 3053/423; a—general view (× 8.0), b—head (× 20.0); Uda, Jurassic.
5. *Necronectes aquaticus* sp. nov. (c).
  Holotype PIN No. 722/23; a—general view (× 2.0), b—fore and middle legs (× 5.0); Ust'-Balei, Jurassic.
6. *Necronectes gigas* sp. nov. (c).
  Holotype PIN No. 2554/477 (× 1.1); Karatau, Upper Jurassic.
7. *Necronectes cyrenaicus* sp. nov. (c).
  Holotype PIN No. 3394/24 (× 1.4); Bryanka, Lower Cretaceous.
8. ? *Necronectes latus* sp. nov. (c).
  Holotype PIN No. 3072/151* (× 5.5); Shurab III, Jurassic.

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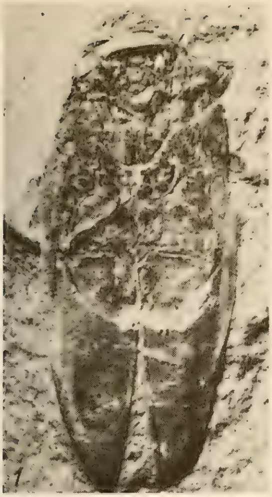
*Given as 3073/151 in the text and Figure 7—General Editor.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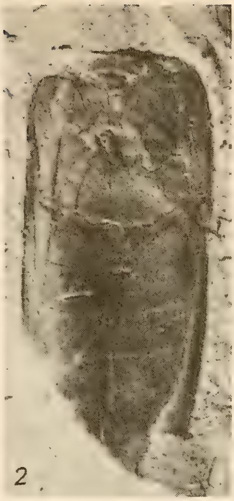
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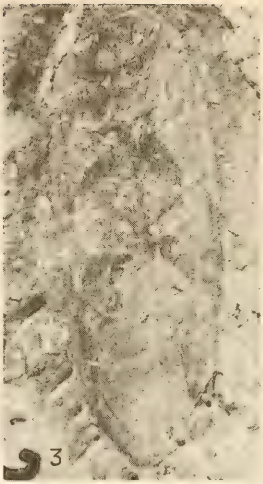
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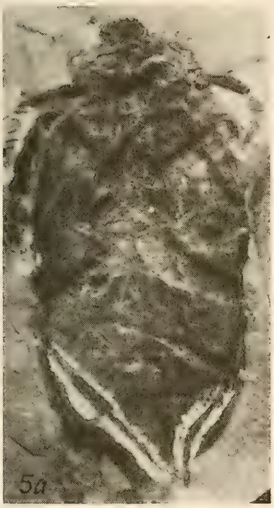
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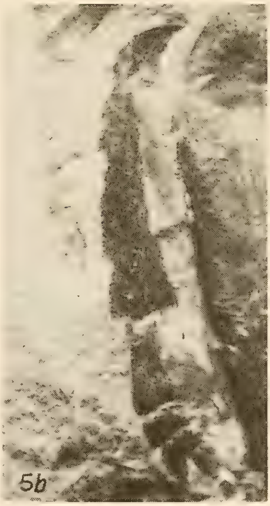
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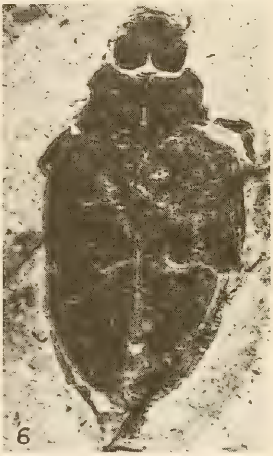
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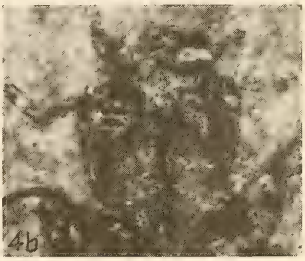
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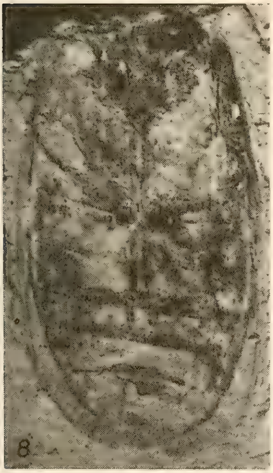
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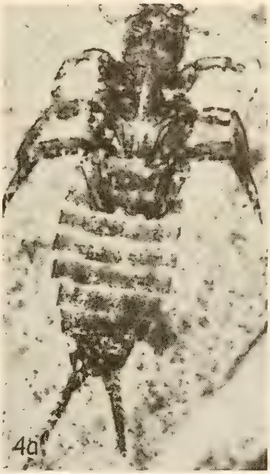
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PLATE II

Family Coptoclavidae

1. *Exedia plana* sp. nov. (c)
   Holotype PIN No. 2554/778 (× 1.7); Karatau, Upper Jurassic.

2 and 3. *Stygeonectes jurassicus* sp. nov. (c)
   Paratype: 2—PIN No. 3000/939 (× 10.0); 3—PIN No. 3000/986; a—(× 6.0), b— Head (× 20.0); Novospasskoe, Jurassic.

4 and 5. *Charonoscapha grossa* sp. nov. (c)
   4—Holotype PIN No. 2554/446; a—(× 2.5), b— head and pronotum (× 4.0); 5—Paratype PIN No. 2997/1847 (× 2.5); Karatau, Upper Jurassic.

6 and 7. *Charonoscapha ovata* sp. nov. (c)
   6—Holotype PIN No. 2997/1845 (× 4.0); 7—Paratype PIN No. 2066/2313* (× 3.1); Karatau, Upper Jurassic.

8. *Charonoscaphidia elongata* sp. nov. (c)
   Holotype PIN No. 2384/717 (× 2.7); Karatau, Upper Jurassic.

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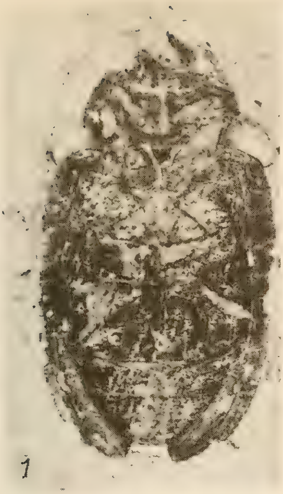
*Given as 2066/2393 in the text and Figure 11—General Editor.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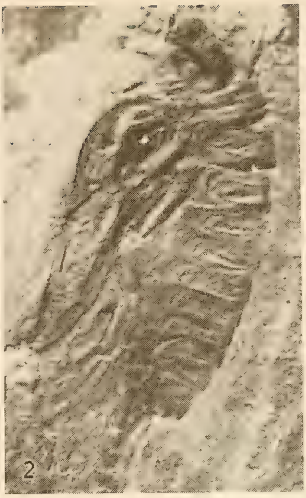
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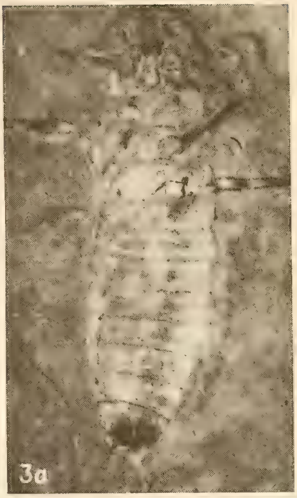
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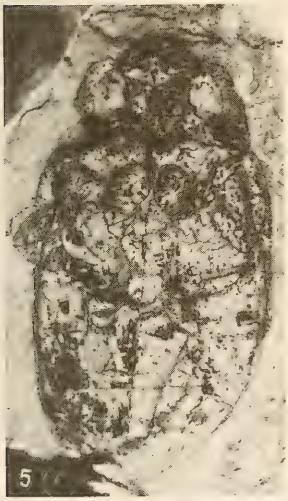
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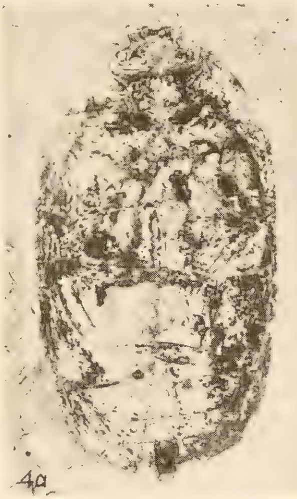
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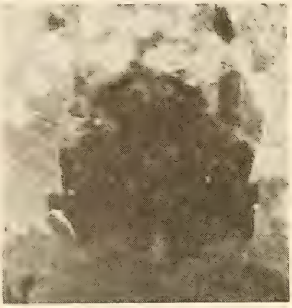

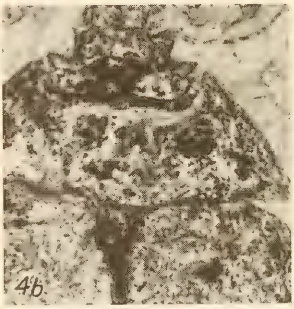
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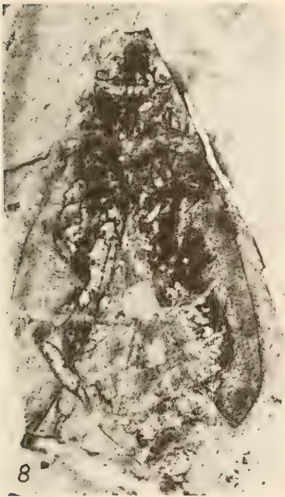
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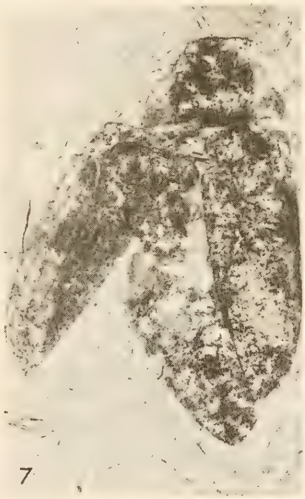
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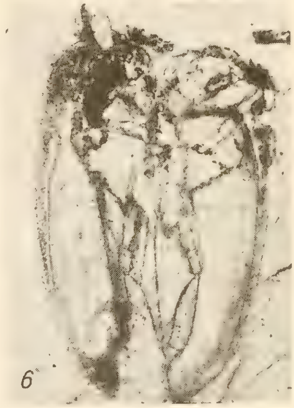
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PLATE III

Families Liadytidae, Dytiscidae and Gyrinidae

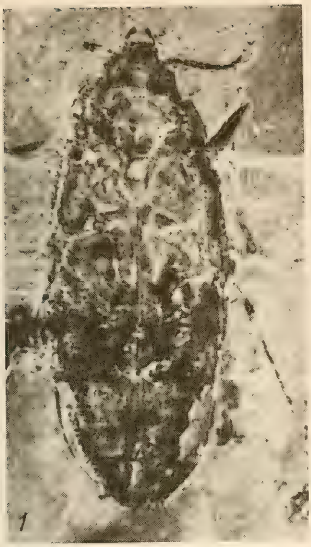
1. *Liadytes longus* sp. nov. (c)
   Holotype PIN No. 2046/1 (× 2.0); Daya, Lower Cretaceous.
2. *Liadytes crassus* sp. nov. (c)
   Holotype PIN No. 3015/369 (× 10.0); Unda, Lower Cretaceous.
3. *Cretodytes latipes* sp. nov. (c)
   Holotype PIN No. 2383/256 (× 6.0); Kyzyl-Dzhar, Upper Cretaceous.

200 4. *Avitortor primitivus* sp. nov. (c)
   Holotype PIN No. 3064/856 (× 6.3); Baisa, Lower Cretaceous.

5 and 6. *Mesodyneutes amurensis* sp. nov. (c)
   5—Holotype PIN No. 2055/74 (× 5.0). 6— Paratype PIN No. 2055/79 (× 6.5); Arkhara, Upper Cretaceous.

7. *Angarogyrus minimus* sp. nov. (c)
   Holotype PIN No. 1874/30 (× 11.8); Iya, Jurassic.
8. *Cretotortor archarensis* sp. nov. (c)
   Holotype PIN No. 2055/75 (× 6.5); Arkhara. Upper Cretaceous.
9. *Triadogyrus sternalis* sp. nov. (c)
   Holotype PIN No. 3320/131* (× 5.4); Garazhovka, Upper Triassic.

*Given as 3320/13 in the text and Figure 53—General Editor.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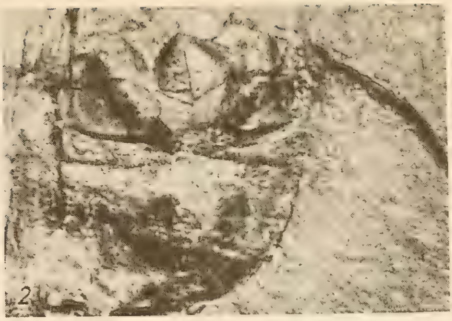
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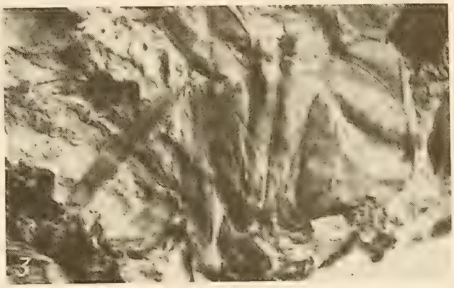
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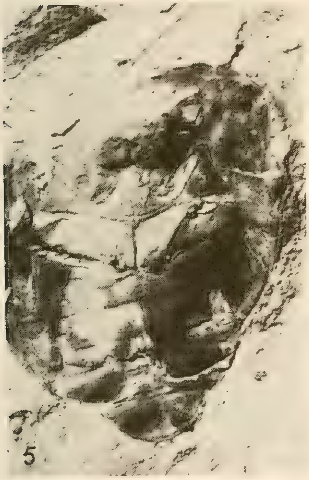
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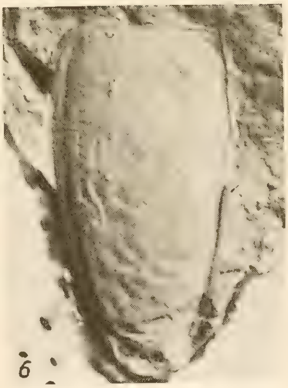
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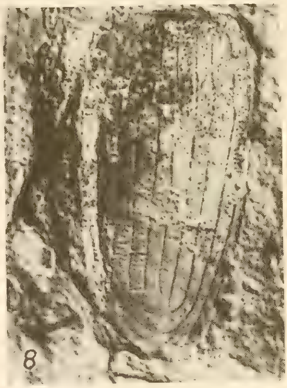
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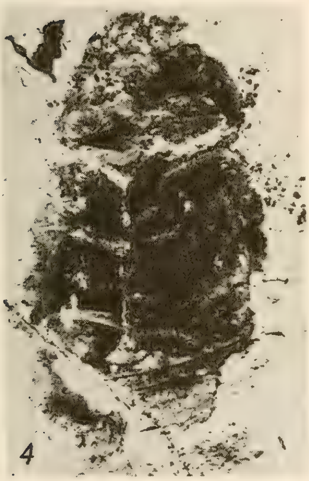
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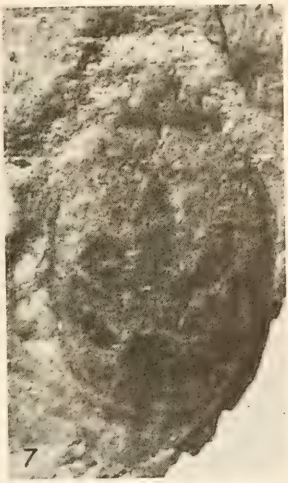
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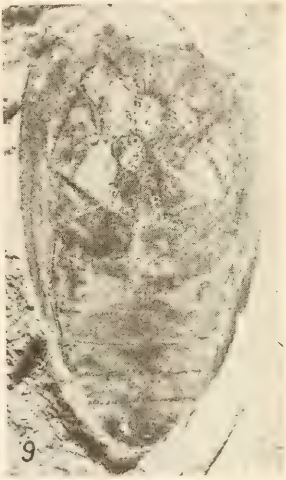
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PLATE IV

Family Trachypacheidae

1. *Sogdodromeus altus* sp. nov. (c)
   Holotype PIN No. 2971/1417* (× 6.5); Madygen Triassic.
2. *Platycoxa armata* sp. nov. (c)
   Holotype PIN No. 2903/222 (× 7.5); Issyk-Kul', Lower Jurassic.
3. *Platycoxa jurassica* sp. nov. (c)
   Holotype PIN No. 2997/6** (× 9.2); Kenderlyk, Lower Jurassic.
4. *Unda microplata* sp. nov. (c)
   Holotype PIN No. 3015/371 (× 10.0); Unda, Lower Cretaceous.
5. *Unda angulata* sp. nov. (c)
   Holotype PIN No. 2372/24 (× 10.0); a—prothorax; b—metathorax and abdomen; Daya, Lower Cretaceous.
6. *Unda cursoria* sp. nov. (c)
   Holotype PIN No. 2372/23 (× 6.5); Daya Lower Cretaceous.
7. *Psacodromeus gutta* sp. nov. (c)
   Holotype PIN No. 2554/456 (× 5.0); Karatau, Upper Jurassic.
8. *Psacodromeus ovalis* sp. nov. (c)
   Holotype PIN No. 2997/1849 (× 5.7); Karatau, Upper Jurassic.

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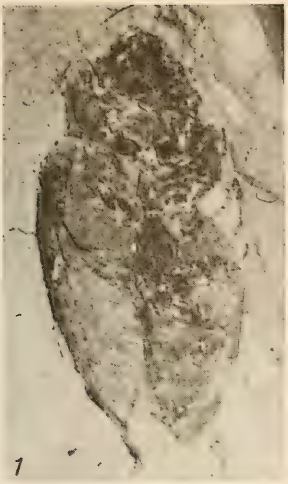
*Given as 2971/417 in the text and Figure 21—General Editor.

**Given as 2496/6 in the text and Figure 22b—General Editor.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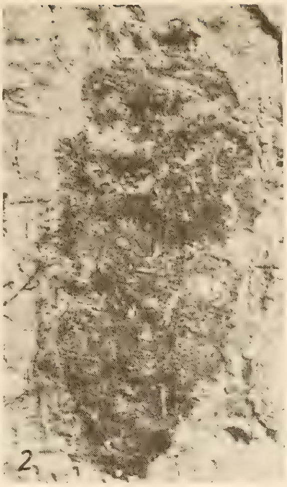
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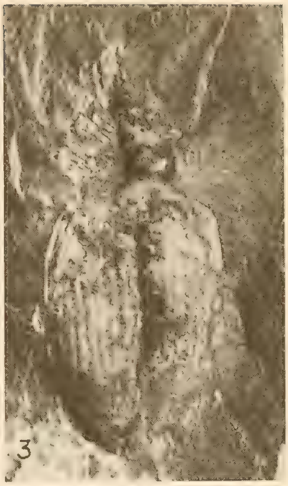
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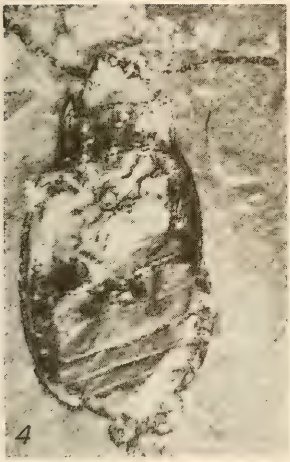
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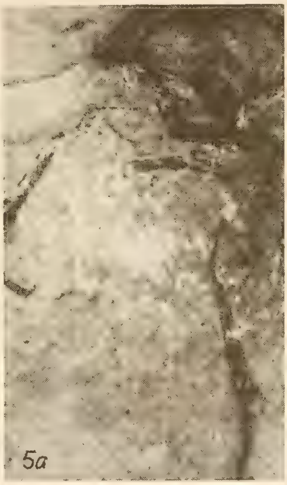
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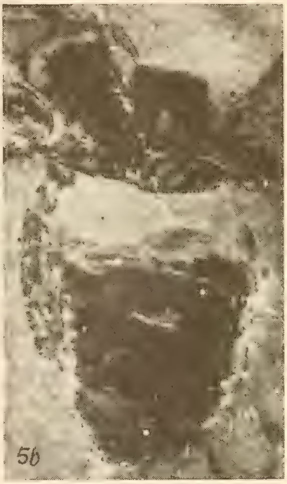
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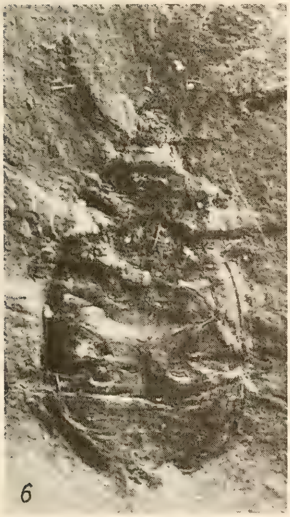
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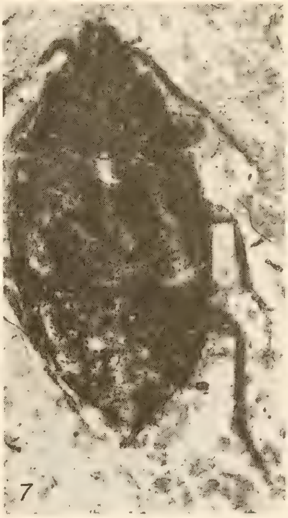
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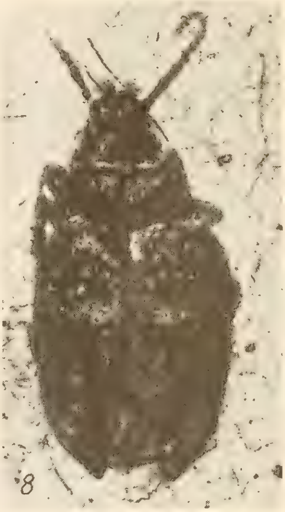
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PLATE V

Family Trachypacheidae

1. *Psacodromeus crassus* sp. nov. (c)
   Holotype PIN No. 2066/3147 (× 8.6); Karatau, Upper Jurassic.
2. *Psacodromeus rugosus* sp. nov. (c)
   Holotype PIN No. 1789/214 (× 4.4); Karatau, Upper Jurassic.
3. *Karatoma agilis* sp. nov. (c)
   Holotype PIN No. 2784/1528 (× 2.5); Karatau, Upper Jurassic.
4. *Karatoma raptor* sp. nov. (c)
   Holotype PIN No. 3015/362 (× 5.2); a—reverse impression; b—direct impression; Unda, Lower Cretaceous.
5. *Karadromeus rostratus* sp. nov. (c)
   Holotype PIN No. 2904/873 (× 8.0); Karatau, Upper Jurassic.
6. *Karadromeus latus* sp. nov. (c)
   Holotype PIN No. 2384/567 (× 6.7); Karatau, Upper Jurassic.
7. *Karadromeus elongatus* sp. nov. (c)
   Holotype PIN No. 3015/303* (× 13.7); Unda, Lower Cretaceous.
8. *Karadromeus mongolicus* sp. nov. (c)
   Holotype PIN No. 3145/753 (× 7.8); Anda-Khuduk, Lower Cretaceous.

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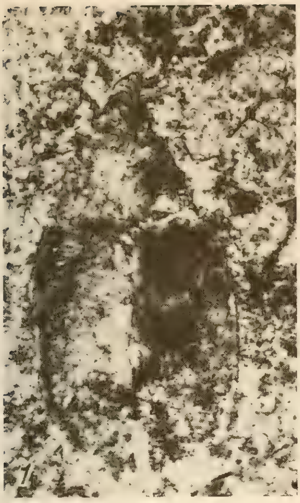
*Given as 3015/363 in the text and Figure 34a—General Editor.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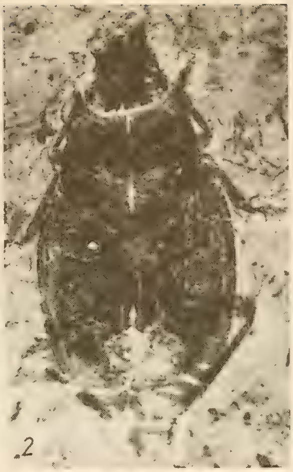
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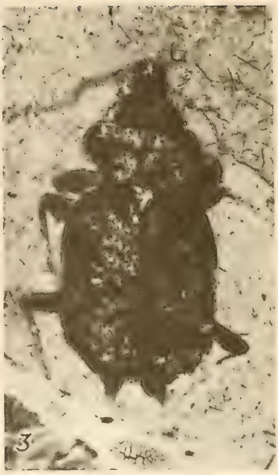
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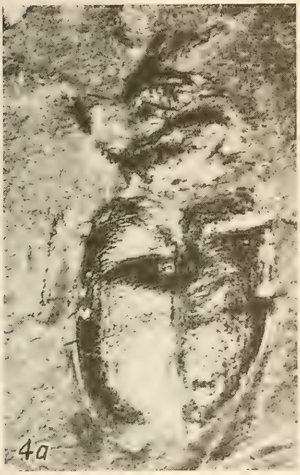
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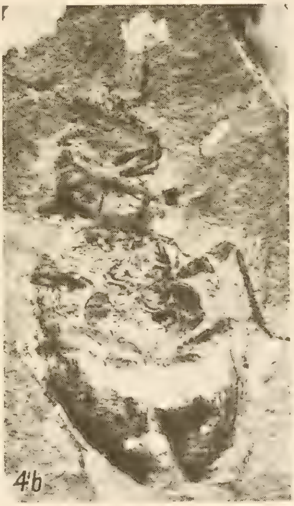
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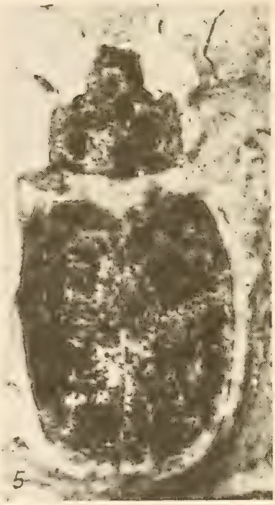
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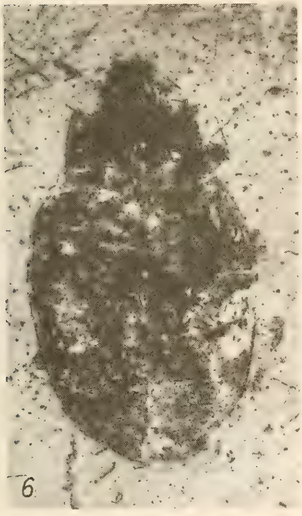
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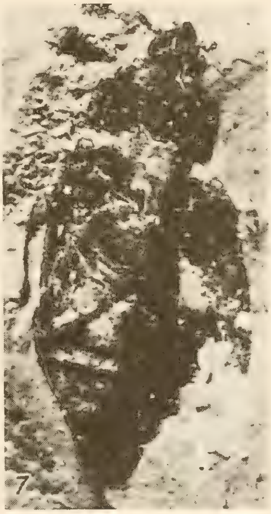
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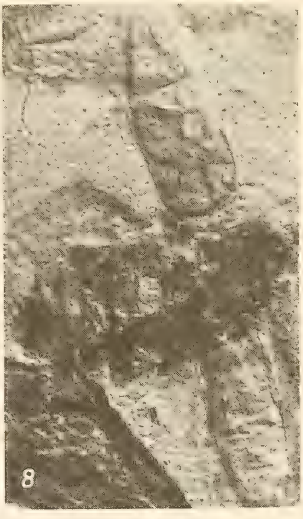
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PLATE VI

Families Trachypacheidae and Carabidae

1. *Eodromeus antiquus* sp. nov. (c)
   Holotype PIN No. 2239/897 (× 6.5): a—reverse impression; b—direct impression; Karatau, Upper Jurassic.

201 2. *Eodromeus sternalis* sp. nov. (c)
   Holotype PIN No. 3191/5 (× 8.0); Chikoiskaya basin, Lower Cretaceous.

3 and 4. *Eodromeus dissectus* sp. nov. (c)
   3—Holotype PIN No. 1989/2976* (× 15.0); 4—Paratype PIN No. 3064/803** (× 7.0); Baisa, Lower Cretaceous.

5. *Eodromeus major* sp. nov. (c)
   Holotype PIN No. 3064/864 (× 4.7); Baisa, Lower Cretaceous.

6 and 7. *Protorabus planus* sp. nov. (c)
   6—Holotype PIN No. 2066/3185 (× 4.1); 7— Paratype PIN No. 2904/928 (× 3.3); Karatau, Upper Jurassic.

8. *Protorabus nigrimonticola* sp. nov. (c)
   Holotype PIN No. 2997/1851 (× 5.8); Karatau, Upper Jurassic.

9. *Protorabus magnus* sp. nov. (c)
   Holotype PIN No. 2554/ 447 (× 3.0); Karatau, Upper Jurassic.

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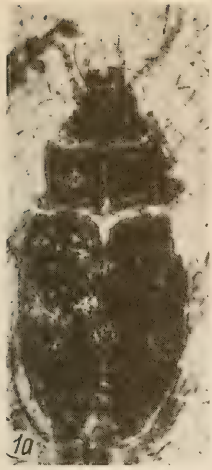
*Given as 1989/2967 in the text and Figure 37a—General Editor.

**Given as 3064/863 in the text—General Editor.



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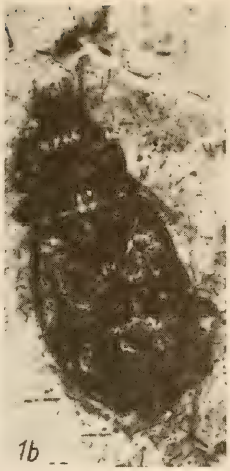

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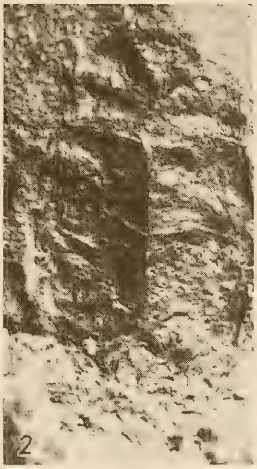

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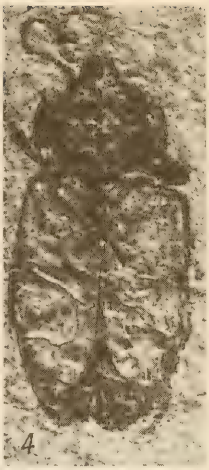

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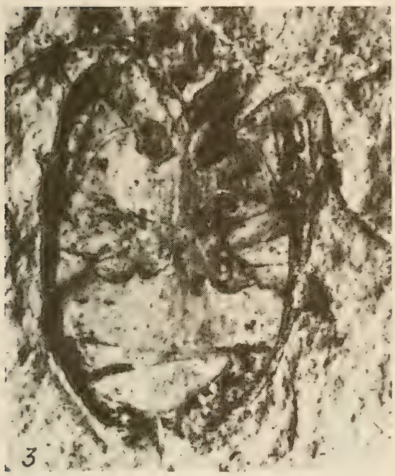

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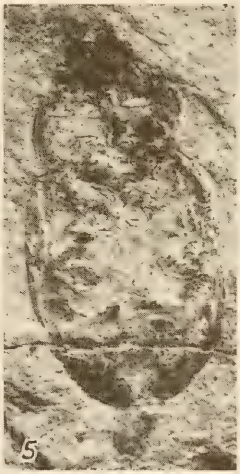

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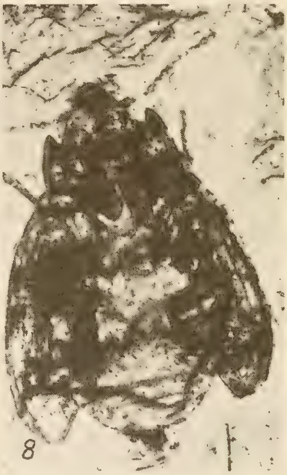

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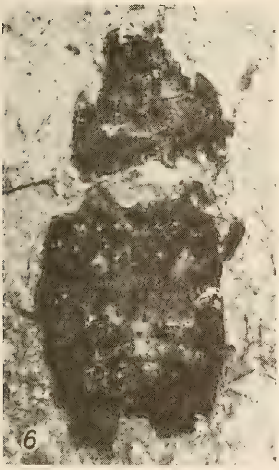

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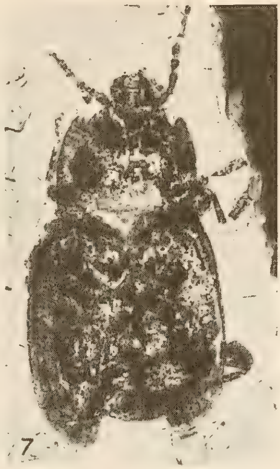

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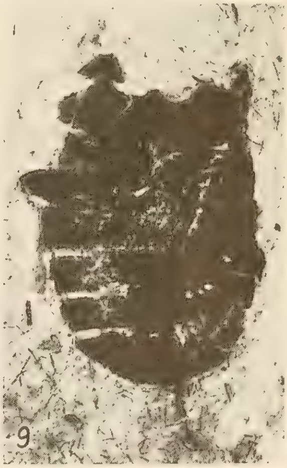

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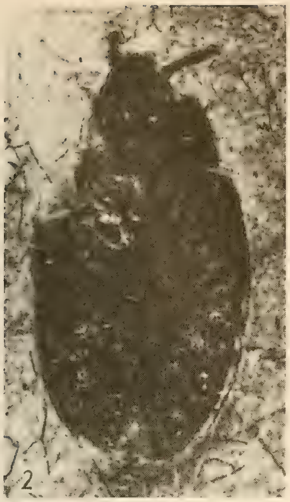
PLATE VII

Family Carabidae

1. *Ovrabites ovalis* sp. nov. (c)
   Holotype PIN No. 2904/872 (× 4.0); Karatau, Upper Jurassic.
2. *Overabites jurassicus* sp. nov. (c)
   Holotype PIN No. 2904/877 (× 10.0); Karatau, Upper Jurassic.
3. *Cordorabus notatus* sp. nov. (c)
   Holotype PIN No. 2066/2739 (× 5.0); Karatau, Upper Jurassic.
4. *Cordorabus antennatus* sp. nov. (c)
   Holotype PIN No. 2066/2363 (× 4.7); Karatau, Upper Jurassic.
5. *Cordorabus minimus* sp. nov. (c)
   Holotype PIN No. 2239/905 (× 10.0); Karatau, Upper Jurassic.
6. *Lithorabus incertus* sp. nov. (c)
   Holotype PIN No. 371/49 (× 16.1); Issyk-Kul', Lower Jurassic.
7. *Cretorabus capitatus* sp. nov. (c)
   Holotype PIN No. 3064/862 (× 9.3); Baisa, Lower Cretaceous.
8. *Cretorabus latus* sp. nov. (c)
   Holotype PIN No. 3064/852 (× 3.2); Baisa, Lower, Cretaceous.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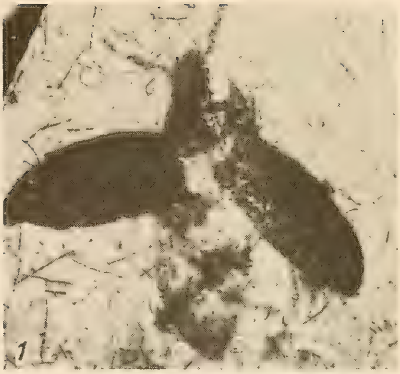
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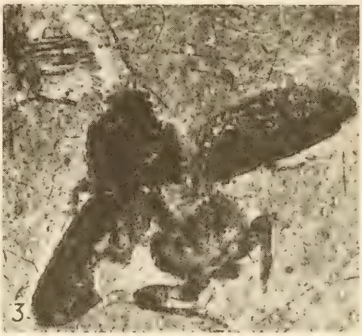
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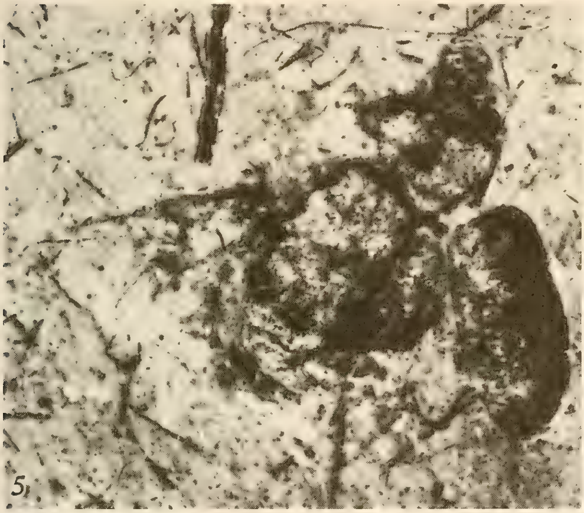
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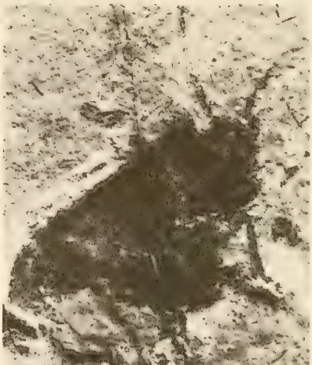
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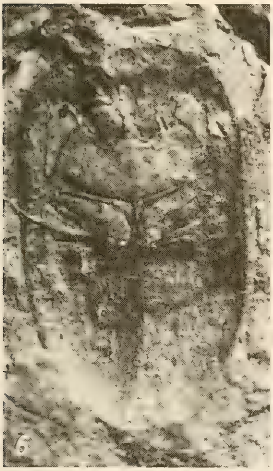
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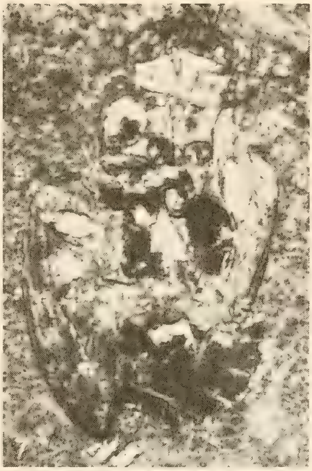
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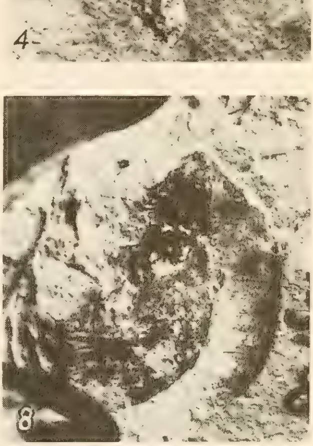
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PLATE VIII

Family, Carabidae, Adephaga Incertae Sedis

1. *Mesorabus elongatus* sp. nov. (c)
   Holotype PIN No. 2784/1525 (× 2.5): a—reverse impression; b—direct impression; Karatau, Upper Jurassic.
2. *Conjunctia prodroma* sp. nov. (c)
   Holotype PIN No. 1668/1763 (× 10.0); Baisa, Lower Cretaceous.
3. "*Carabites*" *vitimensis* sp. nov. (c)
   Holotype PIN No. 3064/871 (× 12.0); Baisa, Lower Cretaceous
4. "*Carabites*" *creta* sp. nov. (c)
   Holotype PIN No. 2383/111 (× 10.8): a—head and pronotum; b—metathorax, Kyzyl-Dzhar, Upper Cretaceous.
5. Harpalinae gen. sp. (c)
   specimen PIN No. 2383/206a (× 14.0); Kyzyl-Dzhar, Upper Cretaceous.
6. *Necronectulus avus* sp. nov. (c)
   Holotype PIN No. 1362/27 (× 12.0); Kenderlyk, Lower Cretaceous.

7—9. *Cretotaenia pallida* sp. nov. (c)
   7—Holotype PIN No. 1989/2890: a—general view (× 7.0); b— head (× 40.0). Paratypes: 8—PIN No. 1989/2889 (× 5.5); 9—PIN No. 1668/1835* (× 5.5); Baisa, Lower Cretaceous.

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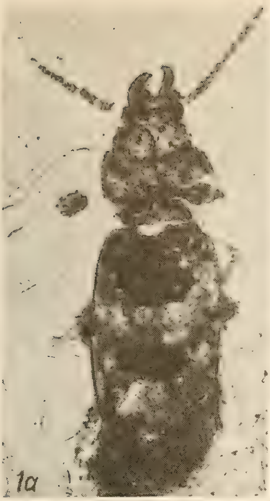
*Given as 1668/1837 in Figure 52e—General Editor.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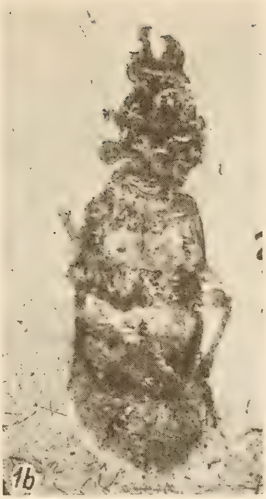
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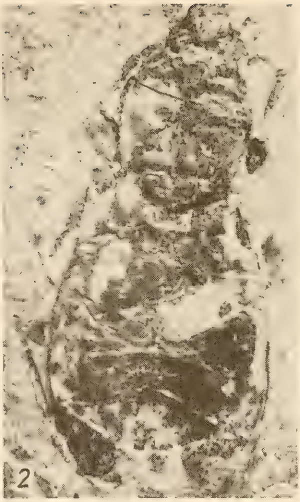
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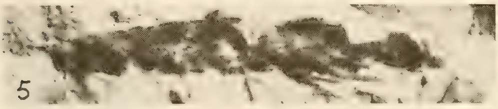
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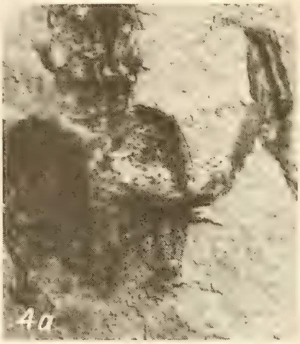
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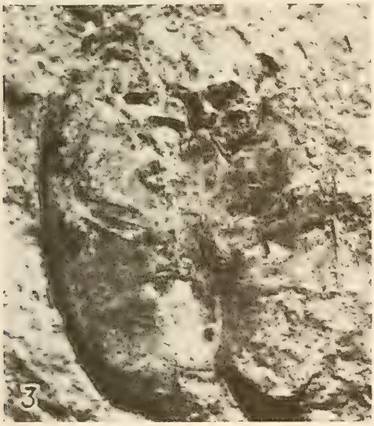
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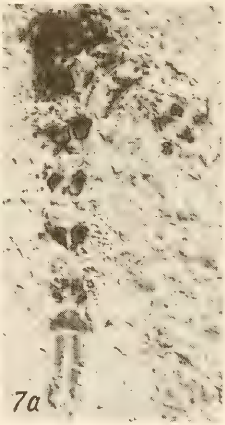
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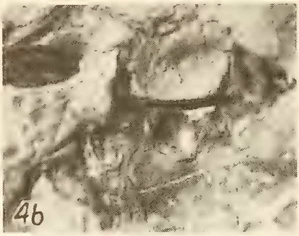
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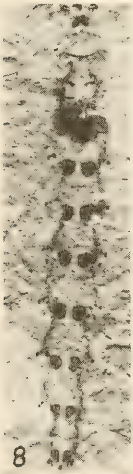
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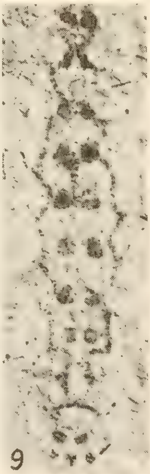
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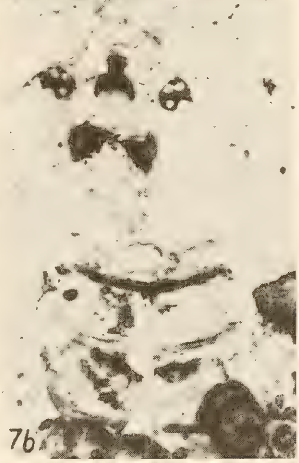
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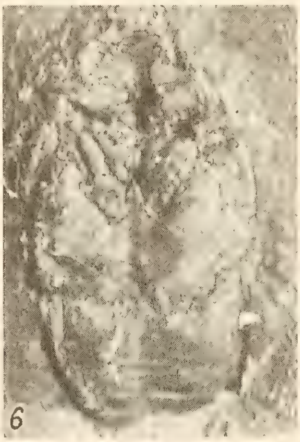
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PLATE IX

Familes Hydraenidae and Hydrophilidae

1. *Peltosyne triassica* sp. nov. (c)
   Holotype PIN No. 2240/278 (× 6.3); Dzhailyaucho, Triassic.
2. "*Ochthebiites*" *altus* sp. nov. (c)
   Holotype PIN No. 3000/917 (× 20.0); Novospasskoe, Jurassic.

3 and 4. *Mesospercheus tarsalis* sp. nov. (c)
   3—Holotype PIN No. 3015/367 (× 8.5); 4—Paratype PIN No. 3063/116 (× 12.5); Unda, Lower Cretaceous.

5. *Mesospercheus notatus* sp. nov. (c)
   Holotype PIN No. 3000/923 (× 6.4); Novospasskoe, Jurassic.
6. *Mesydra elongata* sp. nov. (c)
   Holotype PIN No. 1989/2983 (× 10.0); Baisa, Lower Cretaceous.
7. *Mesohelophorus sibiricus* sp. nov. (c)
   Holotype PIN No. 3064/841 (× 17.0): a—reverse impression; b—direct impression; Baisa, Lower Cretaceous.
8. *Paraspercheus asiaticus* sp. nov. (c)
   Holotype PIN No. 2997/522* (× 4.7); Karatau, Upper Jurassic.
9. *Paraspercheus vitimensis* sp. nov. (c)
   Holotype PIN No. 3064/1071 (× 4.2); Baisa, Lower Cretaceous.

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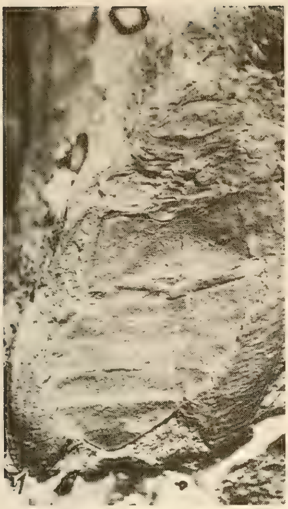
*Given as 2997/552 in the text —General Editor.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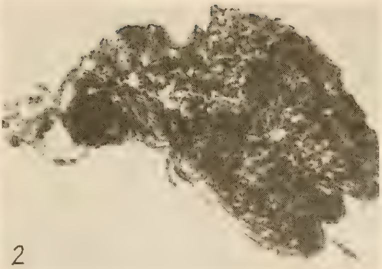
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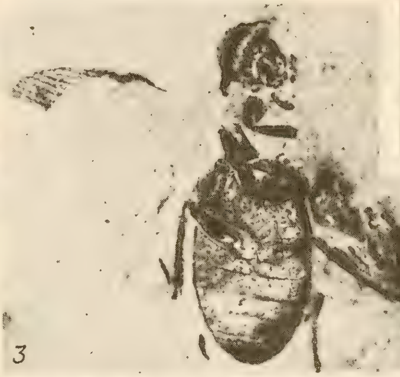
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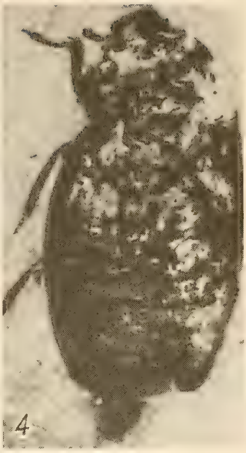
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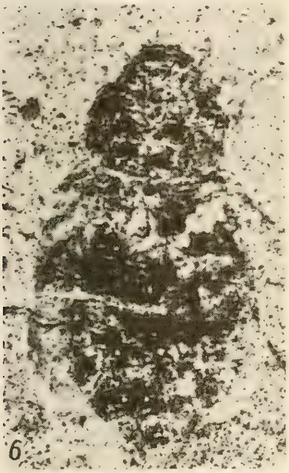
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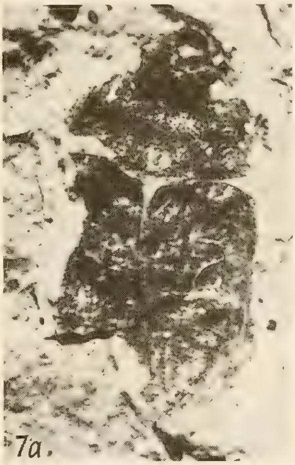
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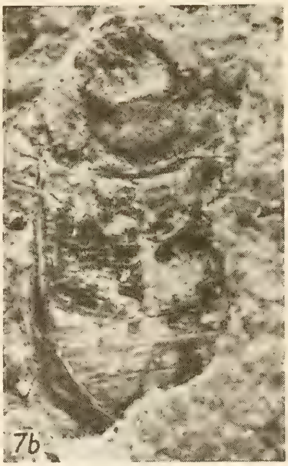
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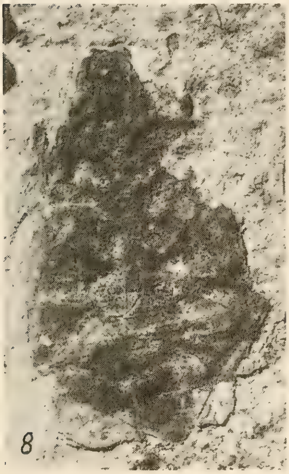
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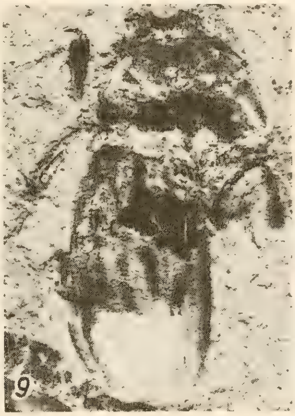
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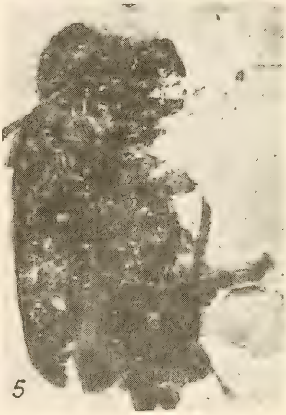
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PLATE X

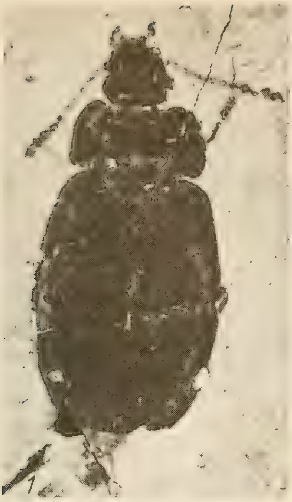
Families Silphidae and Scarabaeidae

1–3. *Mesagyrtes communis* sp. nov. (c)
1—Holotype PIN No. 3000/926 (× 11.0). Paratypes: 2—PIN No. 3000/913 (× 13.0); 3—PIN No. 3000/915 (× 18.0). Novospasskoe, Jurassic.

4 and 5. *Geotrupoides sulcatus* sp. nov. (c)
4—Holotype PIN No. 1668/1785 (× 10.0); a—reverse impression; b—direct impression; 5—Paratype PIN No. 3064/867 (× 10.0); Baisa, Lower Cretaceous.

6. *Geotrupoides leptoscelis* sp. nov. (c)
Holotype PIN No. 3064/936 (× 10.0); a—reverse impression; b—direct impression; Baisa, Lower Cretaceous.

7. *Geotrupoides vitimensis* sp. nov. (c)
Holotype PIN No. 1668/1805 (× 6.8); Baisa, Lower Cretaceous.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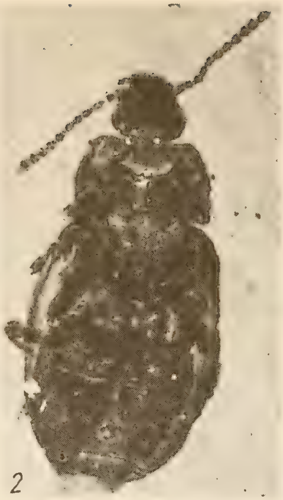
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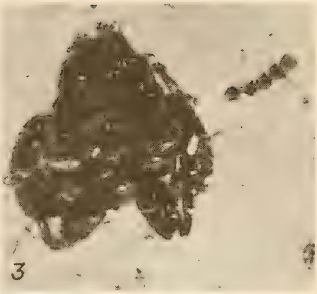
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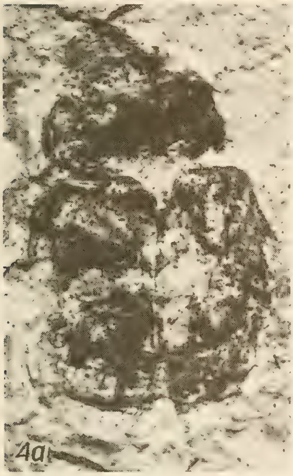
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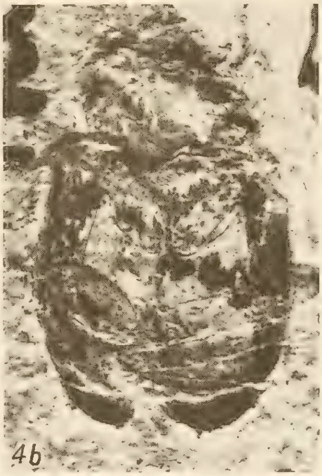
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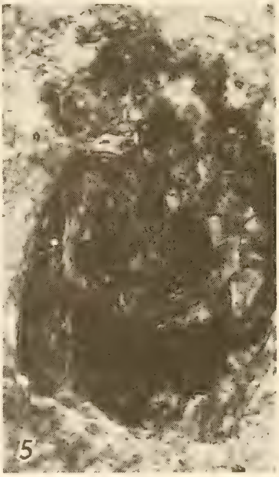
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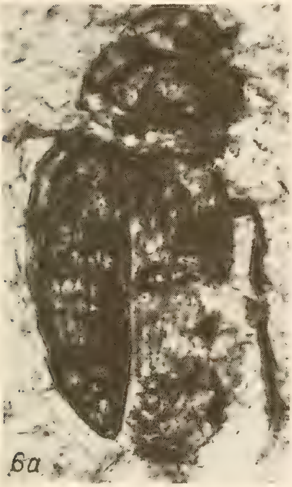
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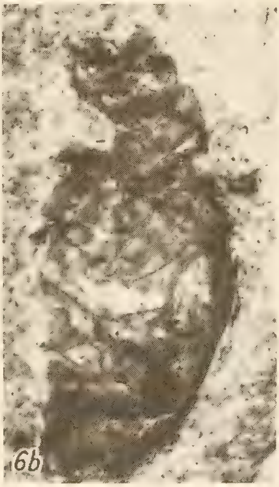
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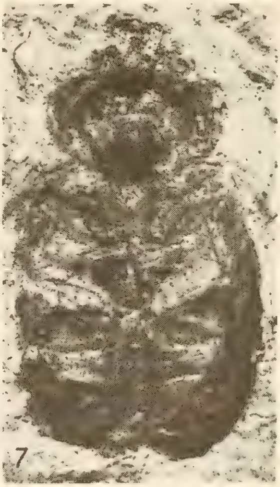
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PLATE XI

Family Scarabaeidae

1–4. *Proteroscarabeus baissensis* sp. nov. (c)
  1— Holotype PIN No. 1668/1830 (× 1.9). Paratypes: 2—PIN No. 1668/2885* (× 3.0); 3—PIN No. 1668/761** (× 3.0); 4—PIN No. 3064/1072 (× 2.2); Baisa, Lower Cretaceous.

5 and 6. *Proteroscarabeus yeni* Grabau (c)
  5—Specimen PIN No. 2385/2 (× 2.0); Semen depression, Lower Cretaceous; 6—specimen PIN No. 1989/2638 (× 10.0); Baisa, Lower Cretaceous.

7. *Holcorobeus vittatus* sp. nov. (c)
  Holotype PIN No. 3064/939 (× 5.4); Baisa, Lower Cretaceous.

8. *Holcorobeus picturatus* (c)
  Holotype PIN No. 1989/2994 (× 4.1); Baisa, Lower Cretaceous.

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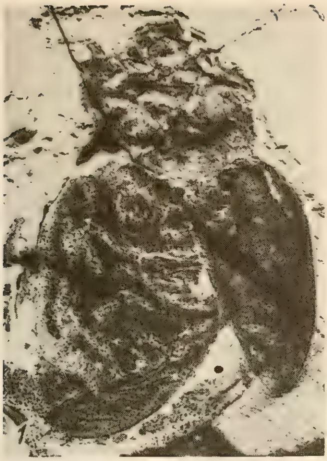
*Given as 1989/2885 in the text and Figure 68b—General Editor.

**Given as 1668/1761 in the text and Figure 68c—General Editor.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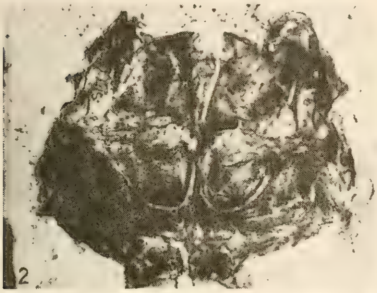
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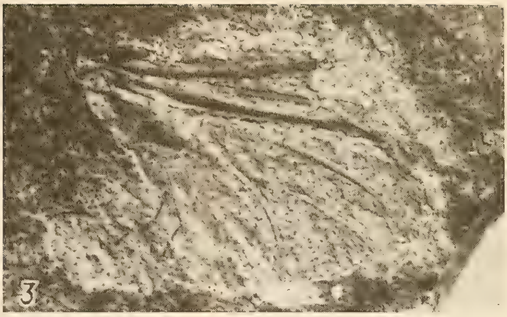
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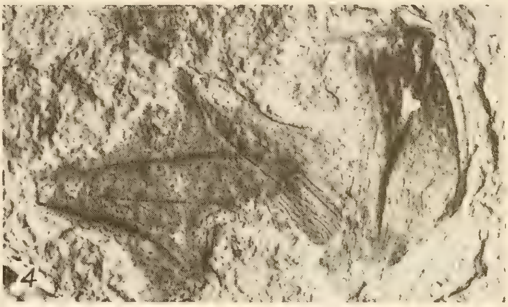
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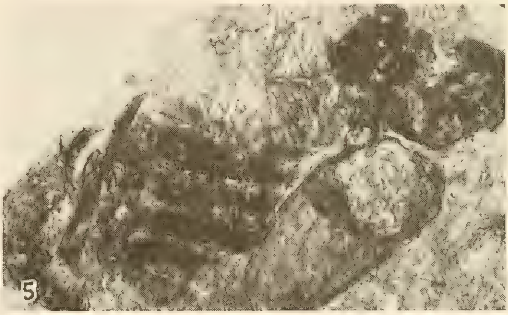
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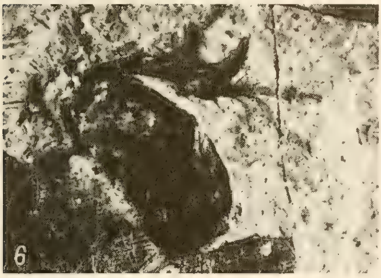
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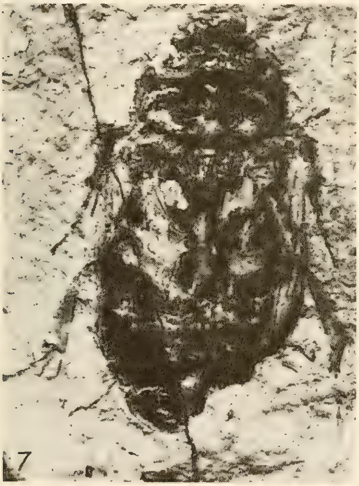
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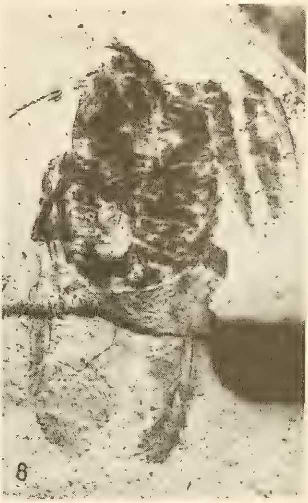
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PLATE XII

Families Cerophytidae, Acanthocnemidae, Cryptophagidae and Eobelidae

1. *Aphytocerus communis* sp. nov. (c)
   Holotype PIN No. 3311/41; a—anterior part of body (× 30.0); b—genitalia (× 47.0); Yantardakh, Upper Cretaceous.
2. *Acanthocnemoides sukatshevae* sp. nov. (c)
   Holotype PIN No. 3308/1 (× 27.9); Zhdanikha, Cretaceous.
3. *Naganasania khetica* sp. nov. (c)
   Holotype PIN No. 3311/45 (× 28.0); Yantardakh, Upper Cretaceous.
4. *Succinimontia infleta* sp. nov. (c)
   Holotype PIN No. 3311/31* (×45.5): a—ventral view; b—dorsal view; Yantardakh, Upper Cretaceous.

203 5. *Eobelus longipes* sp. nov. (c)
   Holotype PIN No. 2452/275 (× 5.4); Karatau, Upper Jurassic.
6. *Archaeorrhynchus paradoxopus* sp. nov. (c)
   Holotype PIN No. 2554/715** (× 3.8); Karatau, Upper Jurassic.

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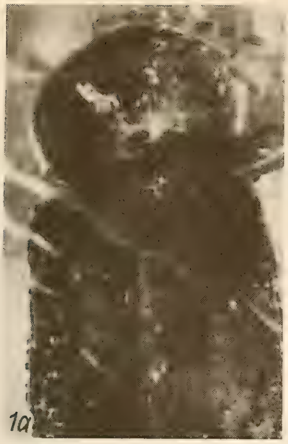
*Given as 3130/31 in the text—General Editor.

**Given as 2335/42 in the text and Figure 79—General Editor.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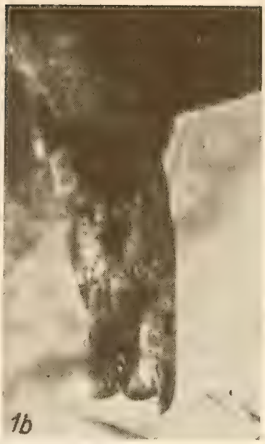
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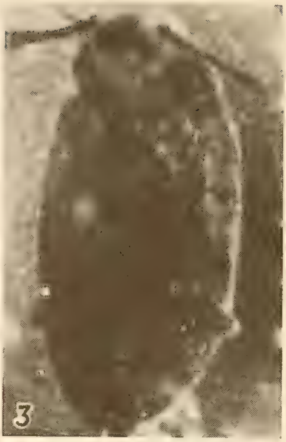
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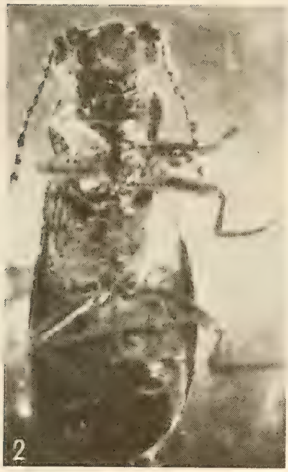
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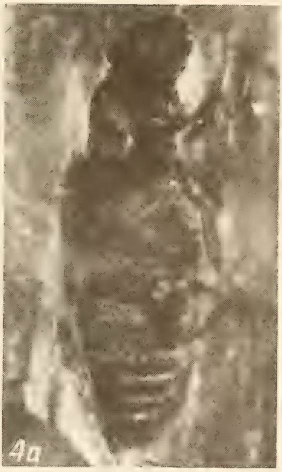
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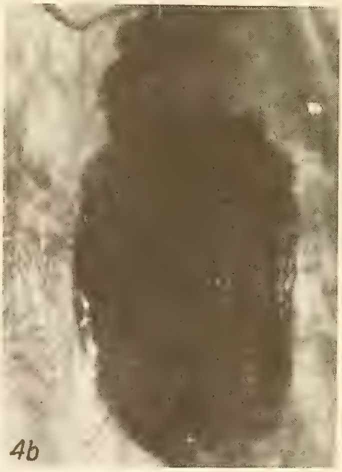
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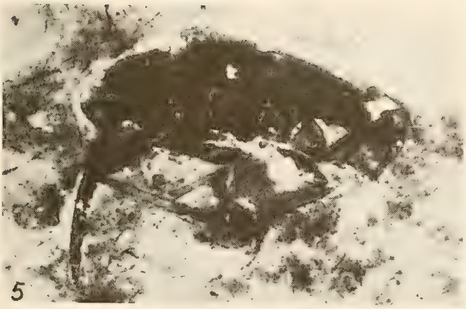
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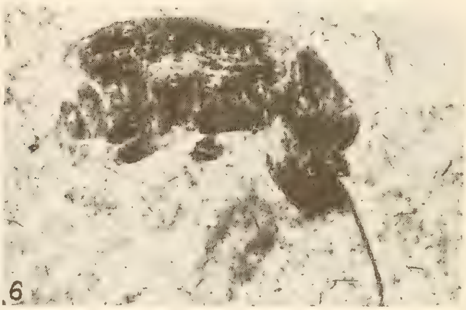
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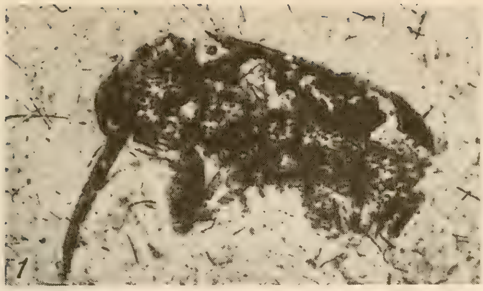
PLATE XIII

Family Eobelidae

1. *Probelus curvispinus* sp. nov. (c)
   Holotype PIN No. 2554/709 (× 6.0).
2. *Probelopsis acutiapex* sp. nov. (c)
   Holotype PIN No. 2239/1554 (× 5.5).
3. *Belonotaris punctatissimus* sp. nov. (c)
   Holotype PIN No. 2452/422* (× 2.4).
4. *Procurculio fortipes* sp. nov. (c)
   Holotype PIN No. 2066/2339 (× 5.6).
5. *Eccoptothorax latipennis* sp. nov. (c)
   Holotype PIN No. 2554/720 (× 6.6)
6. *Oxycorynoides similis* sp. nov. (c)
   Holotype PIN No. 2554/713 (× 15.0)
7. *Scelocamptus tenuirostris* sp. nov. (c)
   Holotype PIN No. 2554/732 (× 4.5).

All the specimens shown on this plate are from Karatau, Upper Jurassic.

*Given as 2462/422 in Figure 85—General Editor.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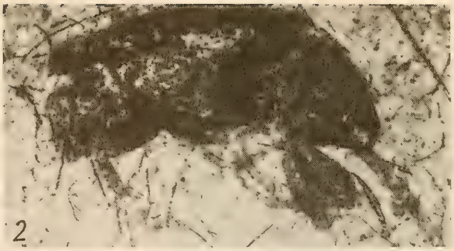
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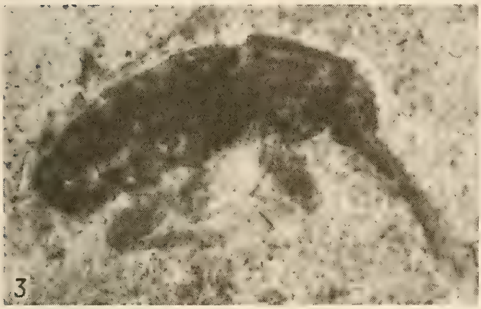
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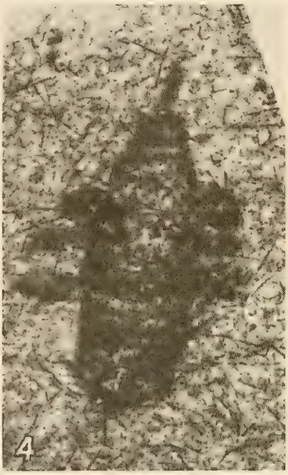
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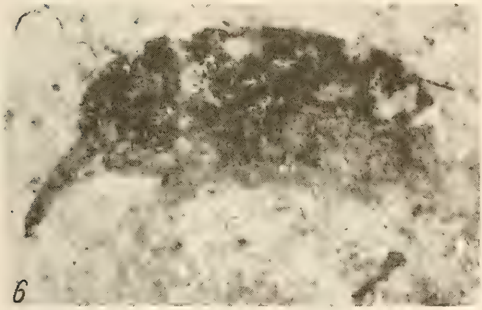
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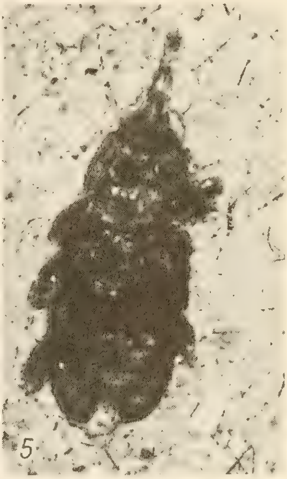
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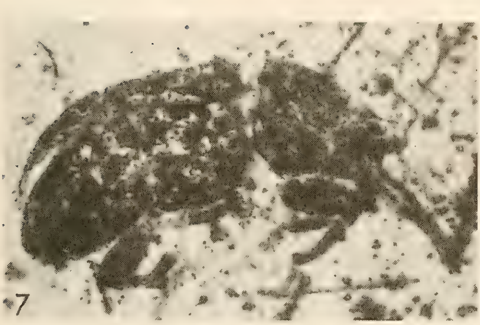
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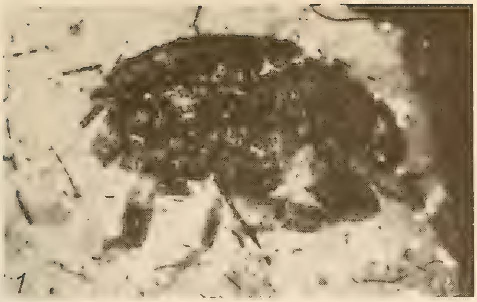
PLATE XIV

Families Eobelidae, Attelabidae and Curculionidae

1. *Ampliceps dentitibia* sp. nov. (c)
   Holotype PIN No. 2239/1562 (× 17.2); Karatau, Upper Jurassic.
2. *Paroxycorynoides elegans* sp. nov. (c)
   Holotype PIN No. 2452/125 (× 10.0); Karatau, Upper Jurassic.
3. *Eccoptarthrus crassipes* sp. nov. (c)
   Holotype PIN No. 2239/1507 (× 7.5); Karatau, Upper Jurassic.
4. *Distenorrhinus angulatus* sp. nov. (c)
   Holotype PIN No. 2239/1547 (× 12); Karatau, Upper Jurassic.
5. *Brenthorrhinus mirabilis* sp. nov. (c)
   Holotype PIN No. 2554/708 (× 7.0); Karatau, Upper Jurassic.
6. *Nanophydes ovatus* sp. nov. (c)
   Holotype PIN No. 1789/102 (× 14.3); Karatau, Upper Jurassic.
7. *Baissorhynchus tarsalis* sp. nov. (c)
   Holotype PIN No. 1989/3010 (× 18.2); Baisa, Lower Cretaceous.
8. *Cretonanophyes longirostris* sp. nov. (c)
   Holotype PIN No. 1668/1772 (× 12.3); Baisa, Lower Cretaceous.
9. *Slonik sibiricus* sp. nov. (c)
   Holotype PIN No. 1989/2938 (× 17.7); Baisa, Lower Cretaceous.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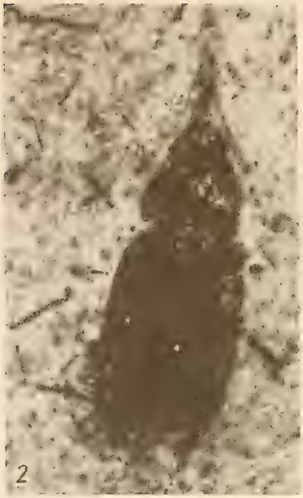
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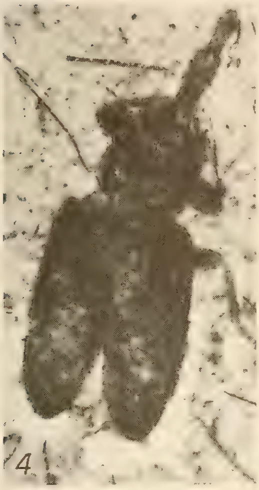
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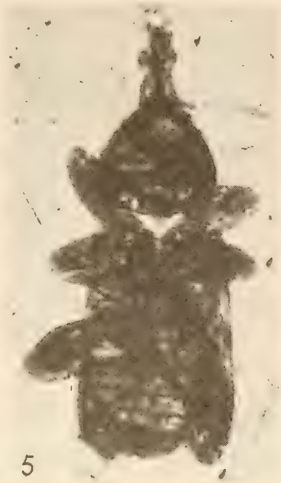
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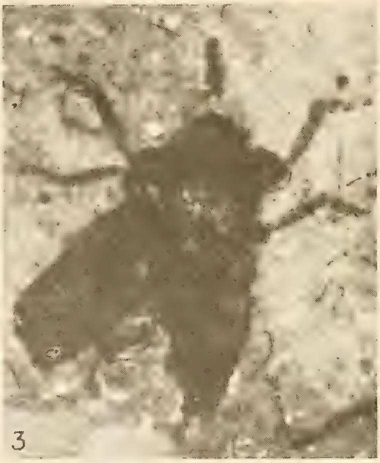
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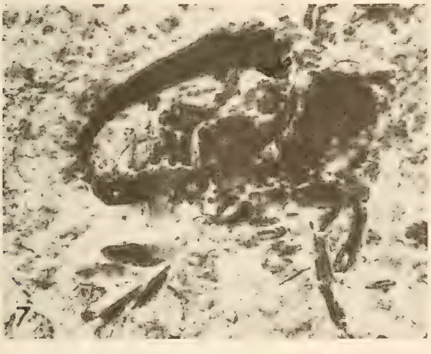
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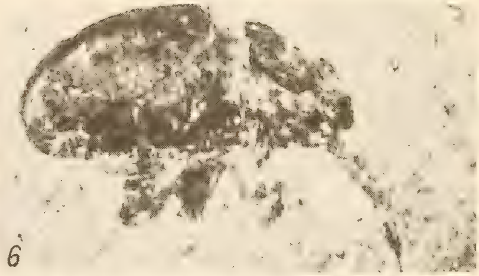
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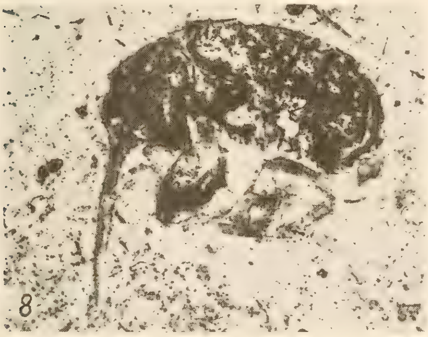
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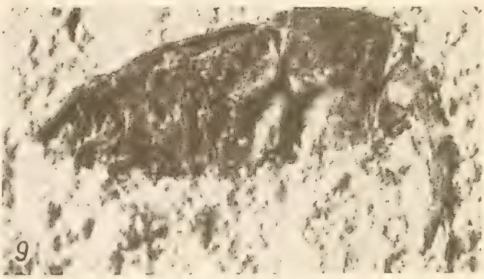
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